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PRINCIPLES OF GENETICS

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PRINCIPLES OF GENETICS

An Elementary Text, with Problems

BY

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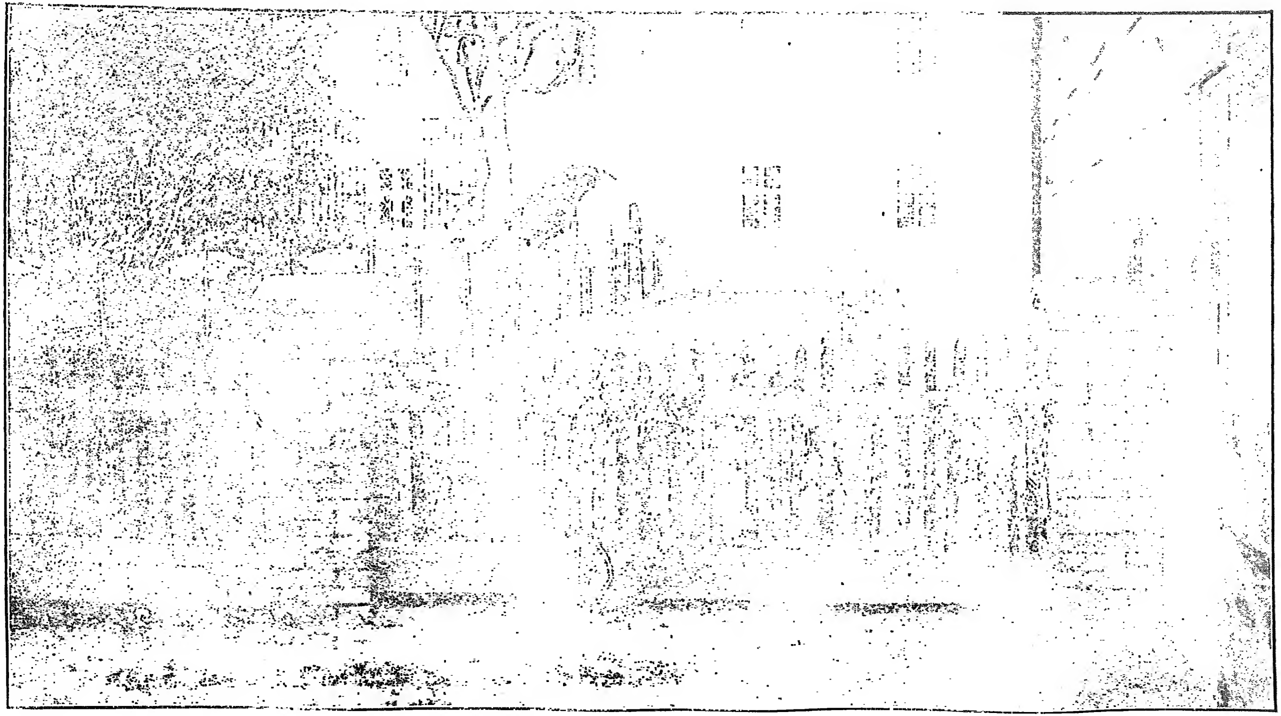
TO THE WORK OF

GREGOR MENDEL

FOR TWENTY-FIVE YEARS A STIMULUS
AND GUIDE TO STUDENTS OF HEREDITY.



Frontispiece. The birthplace of genetics. The garden of the Königskloster, Brünn, where Mendel carried on his experiments with peas. (*Photograph loaned by Prof. G. H. Shull.*)

PREFACE

The object of the present volume is to set forth the essential principles of genetics in as clear and concise a manner as possible.

Genetics is still so young a science and is changing so rapidly from year to year that no uniform practice has been established for the text-book treatment of its subject matter. Difficulties arise in deciding the proper emphasis to be placed on the various topics treated and there is a natural tendency to overstress those particular fields in which the writer's special interests lie. An attempt has here been made to accord each portion of the science such treatment as will result in a well-balanced presentation of the subject as a whole, and this effort has perhaps been aided by the fact that one of the authors is a botanist and the other a zoölogist.

Emphasis throughout has been placed on principles themselves rather than on their practical application. Illustrations and problems have frequently been drawn from plants and animals of economic importance, but only one chapter is devoted to a discussion of the practical bearing of genetics in plant and animal breeding. The experience of the authors indicates that in a one-semester course all that can be attained is a grounding in the fundamentals of the science and that applications had best come in later and more specialized courses. By confining the discussion chiefly to principles it has also been possible to cover the subject in a relatively small volume. To do this, many topics have necessarily been treated very briefly and some have been omitted from the text entirely but taken up, instead, in the Problems or Reference Assignments.

The general plan of presentation is based on the experience of ten years in teaching a course in elementary genetics to college juniors. Every year some change in order, emphasis or method of presentation has been tried and its merits observed in actual practice, the plan here adopted being that which has proved the most satisfactory. The treatment presupposes but little biological knowledge on the part of the student, for even if he has had elementary courses in botany and zoölogy (which is highly desir-

able) it has usually been found necessary to refresh his memory on certain fundamental facts, particularly those concerning cytology and reproduction, in order that he may have a clear understanding of the actual mechanism of inheritance.

Perhaps the most novel feature of the present volume is its series of Questions for Thought and Discussion, Problems and Reference Assignments. The first are designed to stimulate the curiosity and critical judgement of the student and to lead him to a clearer understanding of the principles involved. It should be possible for him to answer them with the aid of such information as is presented in the text. They may profitably be used as the basis for class discussion. The Problems are designed chiefly for laboratory practice. Counting corn kernels, breeding fruit flies and measuring leaves are all valuable laboratory exercises, but for imparting a thorough understanding and mastery of the principles of genetics, and in particular those of mendelian heredity, the experience of the authors has found nothing equal to persistent drill in solving a wide diversity of problems. The problems here offered are perhaps more numerous than can be completed in the ordinary course, and some of them are rather difficult for the beginning student, so that the instructor may wish to omit certain of them. The Reference Assignments are designed to send the student to other sources of information than his text-book and to acquaint him with the main sources of genetic information.

The first ten chapters deal entirely with principles. In Chapter XI are brought together all the several aspects of the problem of variation, including a discussion of the inheritance of acquired characters. Chapter XII suggests the various ways in which the principles of genetics may be of value to the practical breeder, discussing under this head such matters as pure lines, selection, heterosis and inbreeding. The last two chapters, dealing with inheritance in man and the problems of eugenics, have been included in the belief that in most cases the instructor will wish to conclude his course with a study of the application of the principles of heredity to the physical and mental traits of man.

To all those who have been of assistance in the preparation of the text and illustrations the authors desire to express their sincere thanks. Dr. E. M. East, Dr. D. F. Jones, Dr. Paul Mangelsdorf, Dr. Oscar Riddle and Dr. E. C. MacDowell have

been good enough to read portions of the text. A number of our colleagues, particularly Professor G. C. White, have contributed helpful suggestions and information in matters relating to their special fields. To Mr. J. A. Manter the authors are indebted for a number of original photographs. Dr. Walter Landauer, Miss Margaret Schneider and Mrs. L. C. Dunn have rendered valuable service in reading the manuscript and correcting proof, and in other ways. Mr. A. G. Avery has been of assistance in the biometrical work.

The authors are indebted to Dr. E. B. Wilson and the Macmillan Company; to Dr. T. H. Morgan and Henry Holt and Company; to Dr. D. F. Jones and John Wiley and Son; and to Dr. H. H. Newman and the University of Chicago Press for permission to use a number of figures, which are duly acknowledged in each case. They are also under obligation to the editors of *Genetics* and the *Journal of Experimental Zoölogy* for permission to use illustrations from these journals, and to Mr. R. C. Cook, editor of the *Journal of Heredity* for his kindness in supplying a number of photographs originally published in this journal. To the following individuals and organizations, who have been good enough to contribute original photographs or other illustrations, the authors wish to express their grateful thanks: Dr. Sewall Wright and the United States Department of Agriculture; L. R. Crosby and "The Field, Illustrated;" Professor Karl Musser and the Guernsey Cattle Club; H. W. Jackson and the "Reliable Poultry Journal;" the Director of the New Hampshire Agricultural Experiment Station; Col. A. V. Barnes; Dr. A. F. Blakeslee; Dr. C. B. Bridges; Professor W. E. Castle; Professor B. M. Davis, Professor E. M. East; Professor R. A. Emerson; Dr. W. W. Garner; Professor M. F. Guyer; Dr. E. B. Hart; Dr. D. F. Jones; Dr. Laura Kaufmann; Dr. T. B. Osborne; Dr. Oscar Riddle; Dr. Karl Sax; Professor G. H. Shull; Professor C. R. Stockard, and Dr. O. E. White.

The original drawings and diagrams are all by the authors with the exception of Fig. 49, which is by Miss Margaret Schneider.

THE AUTHORS.

STORRS, CONNECTICUT
July, 1925

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FOREWORD

There is a common feeling that a text-book is a full and final exposition of the subject which it treats, and that by virtue of "knowing the book" one acquires all of the knowledge of the subject which it is necessary to have. Such beliefs have little to justify them. No text is or can be complete or final; nor, if it were, would an understanding of the subject be gained by committing the whole book to memory. Knowledge is not acquired in this way, but grows in the minds of those who discover for themselves new facts and relationships.

The principles of genetics have developed out of the arduous study of scores of investigators, and an understanding of them can best be gained by the student through a process which is somewhat similar to that employed in their original discovery. This process begins with and is continually stimulated by curiosity as to the methods and the mechanism of inheritance; it proceeds by the collection and study of facts, and by a critical discrimination between those which are true and relevant and those which are untrue or irrelevant; and finally it involves a considerable practice of the reasoning faculty by which deductions are made, and applied or tested on many similar cases. It is only in this way that the process of inheritance can be *understood.* The learning of facts alone cannot accomplish this.

As an aid to such a comprehension of the science of genetics, this book includes problems of three types, which form an integral part of the subject matter. These are designed to stimulate curiosity, to provide opportunity for practicing and extending the methods and applying the theories outlined in the text, and to point the way to other related facts not specifically treated in this book. They are not designed as memory tests, although the continual use of facts in solving problems is at once the best method of committing these facts to memory as well as of understanding them.

The first of these aids consists of the Questions for Thought and Discussion. Answers to these are not to be found in the text itself, but may be reached by a process of reasoning for

which only the premises are given. Familiarity with the subject matter of the text will provide the raw material, while the synthesis resulting in a correct answer or intelligent discussion must take place in the student's mind.

The Problems themselves are designed to provide more extended practice in reasoning from principles. Nearly all of them require some computation, and may be most profitably studied as laboratory exercises under the guidance of an instructor. It is desirable to use labor-saving or "short-cut" methods (such as the checkerboard method described on page 68) wherever possible in order that the mechanical work involved in calculation may not be regarded as the chief benefit to be derived from them. Sufficient information for solving all of them is contained in the text or in the supplementary notes in the problems.

The Reference Assignments all require study of additional sources, such as the list of books and papers contained in the bibliography (p. 419). They are intended to convince the student that the subject as a whole is not contained in the text but is growing by the continual accretion of reports of experiments, all of which do not yield results in entire consonance with the few points of view which it is possible to present in a brief text-book. Many of the references will lead to new material not mentioned in the text, which must be reconciled with the fundamental principles of genetics, while others may serve to make the connections between the student's knowledge of genetics and his experience in other directions.

PRINCIPLES OF GENETICS

CHAPTER I

THE SCIENCE OF GENETICS

Between those things which are *alive*—plants, animals, and man—and those things which are lifeless, there exists a great gap, which science has not yet bridged. All living things are endowed with certain characteristic properties of structure and of behavior which in the aggregate have been named *Life*, but as to what calls forth this remarkable phenomenon out of lifeless matter, we are still essentially ignorant.

It is known that life is always associated with a characteristic protein substance called *protoplasm*. It is known that protoplasm is not a continuous and homogeneous mass throughout the organism, but is divided into definite though minute units, the *cells*, within each of which is a denser, rounded portion, the *nucleus*. It is known that the body built up from these cells has a very definite shape and structure characteristic of the particular species of which it is a member. It is known that in the various cells of this body complex chemical and physical changes take place whereby growth and repair are effected and the necessary energy for the vital activities of the organism released. It is known that, as a result, the individual successfully maintains itself throughout the course of its normal life history. These various characteristics of living things can be readily observed and described, but thus far there has been less success in understanding and explaining them. Many of the major problems of Biology, that science which deals with life and living things, are yet to be mastered, and to aid in the solution of certain of them is the province of the science of genetics, the principles of which constitute the subject matter of this book.

The Continuity of Life.—It should be understood that living organisms are characterized not merely by the specific peculiarities of form and function which we have just mentioned, but

that their origin is also remarkable. The conclusions reached by all thorough study of the life histories of animals and plants clearly show that every living individual must always arise from some pre-existing living individual and never directly from lifeless matter itself. The work of Pasteur with bacteria and other minute organisms gave the deathblow to the old belief in the "spontaneous generation" of living things out of dead material and proved that even with these most minute organisms the spark of life can be kindled only by life itself. Every animal and plant is therefore to be looked upon as the latest member of a long and uninterrupted succession of living beings, extending back, generation after generation, to the dawn of life. This is the essential teaching of the theory of evolution. The actual origin of life itself is lost in the mists of antiquity, but the pageant of the evolutionary history of living things which unfolds itself in the fossil record of ancient times makes it clear beyond any reasonable doubt that the animals and plants of today are direct lineal descendants of earlier and more primitive types. Continuity is of the essence of life.

Reproduction.—Since individual living things grow old and die, however, this continuity must be maintained by the transmission of life from one individual to a succession of new ones, its offspring. This process is known as *reproduction*, and may be effected in various ways.

In the simplest cases, commonly called *asexual* or *vegetative* reproduction, the body of the parent becomes divided into two or more parts, each of which grows into a new individual. With animals this method is uncommon except in the very simplest types, but among plants the fact that a small portion of the body, when removed and placed under favorable conditions, will often restore the missing parts and establish itself as a new individual, makes multiplication of this type easy and effective both in nature and through the various arts of plant propagation.

Far commoner and more important than this asexual or vegetative method of reproduction, however, is that called *sexual*. An essential feature here is that the function of forming the new individual is delegated to *single cells*, which are set apart for this purpose. Sexual reproduction consists in the *union of two specialized sexual cells or gametes to form one cell*, the fertilized egg or *zygote*, from which develops a new individual. To insure the successful consummation of this process is the function of a

great variety of structures throughout the animal and the plant kingdoms. In all except the lowest forms the gametes themselves are produced in definite reproductive organs, and are of two radically different types; small, usually motile, male gametes and relatively large, non-motile female ones. Among animals the male gametes are known as *sperms* and are produced in a testis, and the female gametes as *eggs* or *ova*, produced in an ovary. At fertilization a sperm and an egg come together and unite, the living substance of one fusing completely with that of the other. The single cell resulting from this union begins to divide, forming a group of cells which develops into an embryo and finally into an adult organism. Among lower plants conditions are essentially like those in animals, although the sexual organs are extremely varied in character. In the higher plants, however, a series of complicated reproductive structures, the flower, fruit, and seed, have been evolved. The male gametes are here produced within the minute *pollen grains* and the female gametes within the *ovules* or potential seeds. The fertilized egg develops into the embryo of the seed.

In all these cases of sexual reproduction the essential thing to recognize is that a parent contributes to each of its offspring only a *single minute cell*, a bit of living substance so small that it is usually far beyond the limit of vision for the unaided eye. This extremely narrow bridge is the only direct physical link between parent and offspring, and across it everything must pass which is transmitted from one generation to the next (Fig. 1).

Heredity.—As a result of this reproductive activity a continuous succession of new individuals arises. One of the most remarkable features of the process is that they *tend to resemble their ancestors very closely*. The offspring of a corn plant develop into corn plants and never into anything else; and those of horses always into horses. Furthermore, any particular kind or variety of corn or horses will produce individuals of just that variety. Even very specific characteristics are often transmitted with great exactness through a long series of generations. In man himself the same phenomenon is no less evident than in the lower organisms. In his own family everyone must have observed instances in which a given trait has been repeatedly passed from parent to child or where it "runs in the family," cropping out here and there in one or a few individuals. This resemblance among individuals related by descent is called *heredity*.

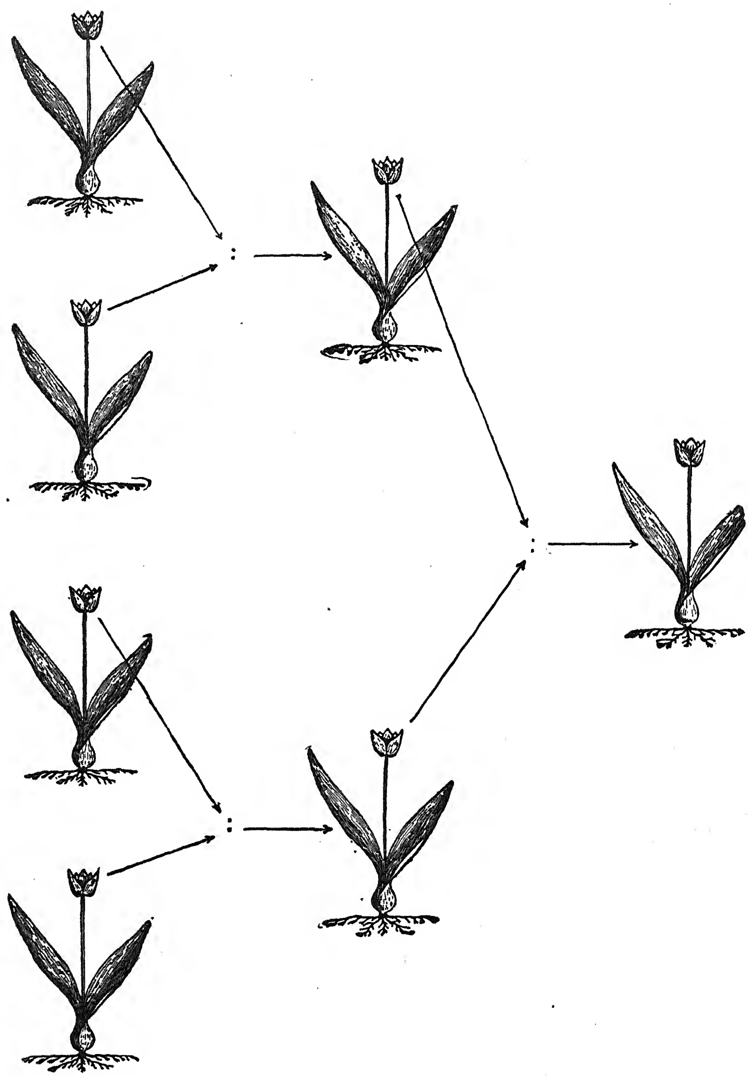


FIG. 1.—The narrow hereditary bridge. The plant at the right receives from each of its parents only one minute sexual cell, a male gamete from one and a female gamete from the other. The parents, in turn, receive from each of the grandparents but one sexual cell. Thus the bridge which connects one generation with the next, and over which the entire inheritance must pass, is an exceedingly narrow one.

Heredity is such a universal and familiar fact that its significance is often not realized. The extremely narrow physical bridge—the reproductive cells or gametes—which connects one generation with the next has already been noted. In the living substance of these tiny sexual elements must in some way be transmitted *all* the characteristics which the new individual inherits from its parents. Any particular adult character, such as size, shape, or color, obviously cannot be found in these cells; but something representing these characters and capable of producing them in the new individual must be there. In the case of man, the color of his eyes, hair, and skin; his susceptibility to various defects and diseases; the size, shape, and proportions of his body; his specific mental traits and capacities, together with many other characteristics, are definitely known to be inherited. In every human sperm, therefore, and in every egg there must be something which represents each of these characteristics and which thus determines what kind of a man or woman will develop from the fertilized egg. These minute particles of living substance, into which so much is packed and out of which so much emerges, are certainly among the most remarkable bits of matter in existence.

Variation.—Close as these hereditary resemblances are, however, they are almost never *exact* resemblances. A group of offspring from the same parents will differ among themselves, and some or all of them may differ from their parents or more remote members of their family. In a group of brothers and sisters no two are exactly alike, but each has his distinctive peculiarities, and although all the children may show resemblances to their parents, they will do so in different degrees. In the lower animals and in plants, where the number of offspring is usually very great, there often seems to be a much closer similarity between individuals, but even here critical study and increased familiarity will in most cases bring differences to light.

These differences are known by the general name of *variations*. Many of them are due to a parcelling out of traits among the various offspring according to a definite method of inheritance. Many others, however, are due to differences in heat, light, moisture, food, or other factors in the environment, for it should be remembered that most characteristics are profoundly affected by the surroundings in which the individual develops. Variations are, therefore, of many kinds and due to many causes, but their

presence is one of the most distinctive features of living organisms and indeed has been said to be the only invariable thing in the organic world.

Genetics and Its History—That branch of the science of biology which is concerned with the phenomena of inheritance and

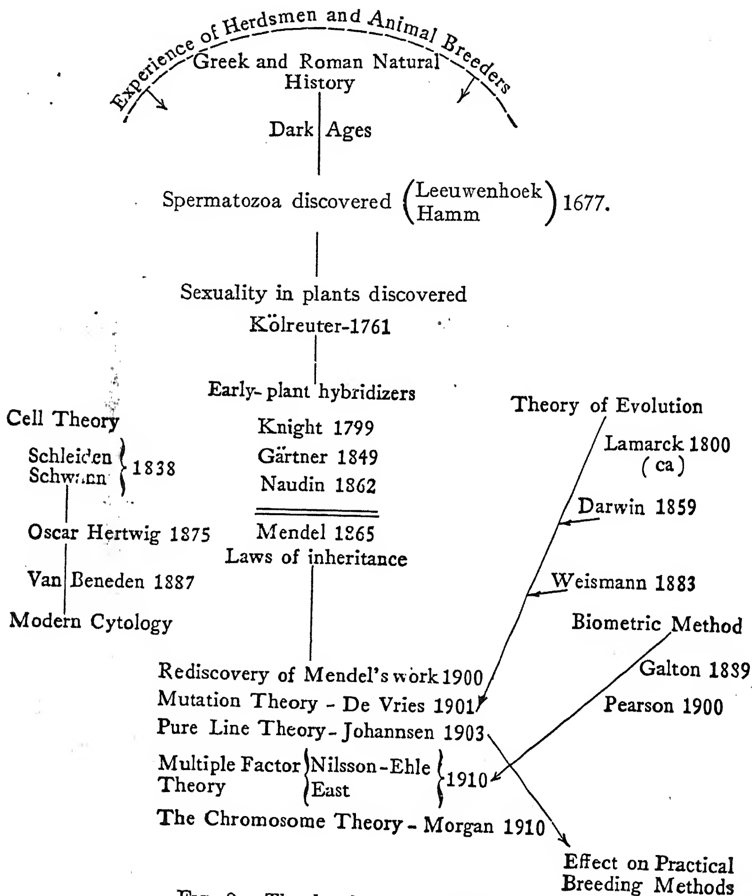


FIG. 2.—The development of genetics.

variation and which particularly endeavors to discover the laws governing these similarities and differences between individuals related to one another by descent is called *genetics*. Unlike most of the other sciences genetics is very young, for as a distinct and recognized branch of knowledge its history goes back only about

a quarter of a century. Development has naturally been rapid during that time, and through the activity of a large number of investigators it is still proceeding apace. The first knowledge of the facts of inheritance, however, began at a much earlier date, and what modern genetics is can perhaps be best understood by going back somewhat into the past (Fig. 2).

From the earliest times men have recognized the facts that "like begets like" and that offspring differ somewhat among themselves and from their parents. They have long used this knowledge, more or less unconsciously, perhaps, in choosing for breeding purposes those individuals among their domesticated animals and plants which best suited their requirements. A scientific understanding of the problems of heredity and variation, however, has begun to be reached only very recently, and has lagged behind knowledge of the other activities of organisms.

The Discovery of Sexuality.—The existence of sexual reproduction among animals was early recognized, as was the fact that offspring inherit their characteristics from both parents. The ideas entertained by the ancients as to the exact mechanism of the process, however, were often grotesque, and it was not until biology was placed on a modern basis, following the invention of the microscope and the establishment of the cell theory, that the existence of gametes and their union in fertilization was determined.

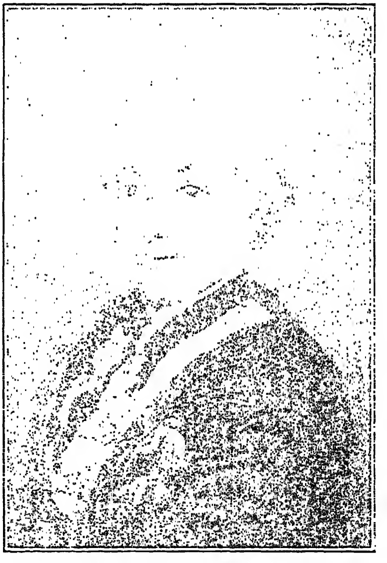


Fig. 3.—Joseph Gottlieb Kölreuter (1733–1806). (*Courtesy of "Genetics."*)

In the plant kingdom the very fact of sexuality was long unknown, as was the important part played by pollen in seed development. In 1760, the German botanist, Kölreuter (Fig. 3), performed the first careful experiments in plant hybridization, crossing two species of tobacco by placing the pollen of one on the stigmas of the other. The offspring resulting from this experiment were intermediate in most respects between the two parent species,

thus proving not only that pollen performed an essential function in seed production but that parental characters were transmitted both through the pollen and through the ovules. The growth of the pollen tube, the passage down it of the male gametes, the union of one of them with the egg cell in the ovule, and the subsequent development therefrom of the embryo of the seed were established at a latter date when microscopical technique had become more highly perfected. Kölreuter performed a number of other experiments in hybridization, endeavoring to find how characters were transmitted from parent to offspring and later generations. He was followed in this work by a group of other pioneers, notably Knight, Gärtner, Naudin, and others. These men were able to establish the facts that offspring of a cross were, in general, intermediate in character between their parents, and that the pollen parent and the seed parent contribute with approximate equality to their offspring. Naudin, however, who in his experimental work was concerned primarily with proving that species are not fixed and immutable, nearly hit upon the great principles of heredity which were to be discovered by Mendel a few years later.

Mendel and His Work.—Gregor Mendel (Fig. 4), whose experiments in plant hybridization laid the foundation for most of the modern work on inheritance and may well be said to have established genetics as a science, was a monk, and later abbot, in the Augustinian monastery at Brünn, Austria. In the cloister gardens there (Frontispiece) he made crosses between varieties of the garden pea which differed in height, flower color, seed color, and other respects. The discoveries which resulted from these experiments were not only due to Mendel's unusual keenness in observation and clarity in reasoning but to several notable improvements in method over his predecessors. He made repeated artificial hybridizations between plants which differed in various characteristics, but instead of studying inheritance in the whole complex individual as a unit, he singled out separate characteristics and observed them by themselves. He also kept accurate pedigree records, which enabled him to know the ancestors of every individual and just what they were like. Perhaps more important still, in all cases where contrasting traits appeared in a group of offspring (both red-flowered and white-flowered plants, for example) he *counted* the number of individuals of each type and thus obtained an exact mathematical

statement of his results. In short, he applied the *experimental method* to the problems of heredity.

The results which Mendel obtained from these hybridization experiments were chiefly notable in showing that inheritance was not a hit-or-miss affair but was subject to certain definite rules or laws; and that, consequently, if one knew enough about the ancestry and constitution of two parent plants, he could predict with a considerable degree of accuracy not only what their offspring would look like but the relative frequency with

FIG. 4.—Gregor Johann Mendel (1822–1884). (*From A. F. Shull.*)

which the contrasting characters, brought in from various ancestral lines, would appear among them. Mendel discovered that the individual behaves in inheritance just as though it were an aggregation of independent and separable characteristics, each of which is a distinct "unit" and may exist with any combination of other characteristics in a given individual. He also found that when two contrasting characters are brought together by a cross, the hybrid offspring are alike and often resemble one of the parents in this particular character much more closely than they do the other. Still more important, if two hybrids are bred

together, both grandparental characteristics appear among the offspring and are sorted out in a definite fashion, a certain proportion of the individuals resembling one grandparent and another resembling the other. The particular combination of characteristics which distinguishes an individual may thus be completely broken up among its descendants, the various traits being sorted out among the offspring entirely independently of one another, so that all sorts of new combinations may make their appearance, each in a definite and predictable fraction of the whole. Mendel thus formulated the first *laws* of inheritance and established the basis on which the later development of genetics has taken place.

Investigations since Mendel.—Important as Mendel's work has proved to modern geneticists, it was not recognized as such by the scientists of his day. His results were collected in a single paper and published in 1866 in a small Austrian journal where they remained in obscurity for over thirty years. Meanwhile the great controversy over the theory of evolution had begun, following the publication of Charles Darwin's "Origin of Species," in 1859, and the attention of biologists was centered upon argument and speculation rather than upon a careful experimental study of plants and animals themselves. Rather fantastic theories, based on little or no experimental evidence, were put forward, one of them by Darwin himself, to explain how parental traits were transmitted to offspring. The facts of heredity and variation were recognized, and indeed the theory of Natural Selection was based upon them, but there was no establishment of anything like general laws of inheritance. This period was not entirely fruitless, however, for the German zoölogist, Weismann, an enthusiastic supporter of Darwin, called attention to the fact that some traits of an individual are due to the inherent characteristics of its living substance and that others are produced by the surroundings in which it has developed. Weismann believed that the latter type, which are now called "acquired" characters, are never inherited, and he performed a series of experiments to determine the fact. This problem of the "inheritance of acquired characters" has since received a great deal of attention, and most of the evidence obtained supports Weismann's contention.

In the last years of the nineteenth century Francis Galton, a cousin of Darwin, became interested in heredity, particularly

in its reference to man. He was the first to apply methods of statistical analysis to the phenomena of variation and heredity and thus established that branch of biological science which is now called *biometry*. Galton devised methods for measuring the degree of resemblance between parents and offspring and endeavored to determine the particular contribution which was made to an individual by each of its ancestors.

At the very end of the nineteenth century interest in the problems of inheritance, which had been steadily growing, was brought to a head by the dramatic discovery and recognition of Mendel's work. It so happened that three botanists, de Vries in Holland, Correns in Germany and Tschermak in Austria, within the same year (1900) independently unearthed Mendel's paper and proclaimed its importance to the world. Many investigators in America and Europe soon began to study the applicability of Mendel's laws to all sorts of plants and animals, and made the youthful science of genetics one of the most active fields of biological research.

It will be impossible here to mention more than a few of the investigators who have made important contributions to genetics during the past twenty-five years or to outline the many advances in interpreting, amplifying and modifying Mendel's principles to conform to the great array of new facts which have been brought to light. The importance of *mutations*, those sudden and unexplained changes in type which sometimes occur in plants and animals, was emphasized by De Vries, whose intensive study of this aspect of genetics led him to propose the mutation theory of evolution, based on a study of large discontinuous variations as opposed to the small and numerous continuous ones chiefly emphasized by Darwin. The variations occurring in plants which from their methods of reproduction (self-fertilization and asexual propagation) provide material for the study of inheritance uncomplicated by hybridization or crossing, were investigated by the Danish botanist, Johannsen. He advanced the pure line hypothesis, which assumes that all individuals descended from a common ancestor by such methods of reproduction have an identical inherited constitution or *genotype*, and will continue to breed true, forming lines genetically pure for all their characters. Characters involving size or quantity, which for the most part do not show sharp and simple mendelian assortment and which in their inheritance were long thought to be exceptions to Men-

del's laws, have been definitely brought into line with the mendelian explanation by the *multiple-factor* hypothesis, independently proposed by East and Nilsson-Ehle. In recent years, greatly increased attention has been given to the minute structure of the cell, and in particular to those remarkable bodies in the nucleus, the *chromosomes;* and knowledge thus gained, supplementing the results from breeding experiments, has thrown much light on the actual mechanism of inheritance. As a result, scientists are beginning to understand such problems as the factors which determine sex, and the peculiar manner in which certain traits tend to stay together or show *linked* inheritance,

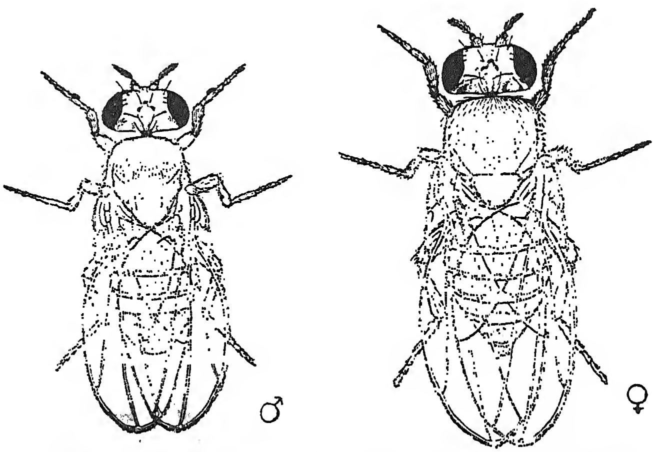


FIG. 5.—Male and female fruit fly, *Drosophila melanogaster.* (*After Morgan.*)

in apparent violation of Mendel's law of independent assortment. To Professor Morgan of Columbia University and his students is due the credit of opening up this new field of genetic research; and the small fruit fly, *Drosophila* (Fig. 5), upon which most of their work has been based, bids fair to assume as great an importance in genetics as the famous peas studied by Mendel.

The Value of Genetics.—Genetics is one of the youngest of the sciences and the various ways in which it may prove its usefulness are, therefore, only beginning to be recognized. In actual dollars-and-cents return this branch of biology has as yet contributed little, but so many fields of human thought and activity involve an application of the principles of inheritance that the science which is concerned with these principles seems destined

to be of very great service in helping to solve some of the most important theoretical and practical problems which confront mankind.

In Agriculture.—The most obvious use to which a knowledge of the principles of genetics may be put is in the field where they first began to be studied—the practical breeding of our domestic animals and plants. Any attempt to measure the money value of genetics to agriculture is as yet premature, for it has scarcely had time to develop and extend the practical application of its theories. The domestication and improvement of valuable animals and plants has been followed by an increase in knowledge of their nutrition, growth, and diseases, and a progessive improvement in methods of care, feeding, and cultivation. Most of these advances have been in the manipulation of the environment and have proved to be of temporary value, calling for renewed efforts in every year or generation. The limit of advance in this direction is being approached, and we are beginning to realize that further progress must be gained chiefly through improvements in the inborn genetic qualities of the animals and plants themselves. Such gains will have the advantage of being permanent, since we know that they may be transmitted to future generations. Already practical breeders, working without the newer knowledge of inheritance, have produced and improved a remarkable array of useful varieties on which our present agriculture is founded, but there is need for further improvement, particularly with respect to such traits as disease resistance which have become more important under modern conditions. Genetics, as such, has already made a few practical contributions to breeding and has aided in the development of several valuable varieties of agricultural animals and plants. Data on the mode of inheritance of such traits as fecundity have been secured, and methods of breeding have been suggested which are now proving useful in practice. Genetics has also been of value in explaining the reasons for the success or failure of many old-established practices, and in subjecting ancient beliefs about breeding to a critical examination by which errors have been corrected, and in some cases unexpected improvements suggested. The ultimate value of genetics to agriculture will probably be found to consist quite as much in the new methods which it introduces and in the general point of view toward plants and animals which it stimulates on the

part of the breeder, as in any specific improvements or additions to his supply of breeds and varieties.

In Human Society.—The advancing knowledge of inheritance is also beginning to prove of value in a field which has seldom been invaded by biology, the improvement of the human race itself. It has become evident that the characteristics of men are subject to the same laws of inheritance which govern the traits of animals and plants. The applied science of *eugenics* is seeking to learn more about these traits, and, on the basis of this knowledge, to devise a program for the improvement of the heritable qualities of mankind. This obviously cannot be accomplished by a direct application of the breeding methods which have been developed with animals and plants, but through the awakening of an intelligent interest in the problem much progress may be made, both in a gradual elimination of defective stocks and in the increase of more desirable human material. Genetics has already weakened the prevalent belief that human traits result chiefly from the action of external or environmental agencies, and has promoted a more general understanding of the fact that forces innate in man are no less important in controlling and directing his fate than are those which originate in his surroundings.

In Scientific Theory.—Important as genetics has been and promises to be in practical matters, its potential contributions to theoretical knowledge are even greater. An understanding of the method of evolution in the animal and plant kingdoms must be based on a knowledge of the way in which traits are transmitted from parents to offspring, and genetic investigation has already been of marked service in leading to a conception of evolution based on experimental evidence rather than on random observation and speculation. An unexpected outcome of genetic research has also been a much more definite knowledge of the structure of living protoplasm itself. Breeding investigations have enabled us not only to identify the chromosomes of the nucleus as the seat of genetic factors but even in some cases to determine the exact position of these factors in the chromosomes.

In Education and Culture.—A study of genetics is useful not only for the reasons which we have enumerated but for its own intrinsic interest and value as well. Perhaps the chief gain to be derived from the pursuit of any science lies in a stimulation of interest and curiosity as to natural phenomena, practice in

inductive reasoning from observed fact to theory, and training in the formation of critical judgments. Genetics is a particularly favorable subject for the exercise of all these faculties because of the peculiar interest which always attaches to the origin and differentiation of living things and of man himself; and because the growing complexity of the facts and theories of inheritance requires, for their mastery, a considerable degree of reasoning power and mental alertness. Genetics, moreover, because of its very youth is developing rapidly, and its results and conclusions, changing in many important respects from year to year, require for their understanding frequent employment of those powers of logical reasoning and critical discrimination which constitute the basis for a scientific attitude toward facts.

QUESTIONS FOR THOUGHT AND DISCUSSION

1. If life can come only from life and if "spontaneous generation" is impossible, where do you think life originated in the first place?

2. Organic life always ends in death. Of what advantage has this fact been in the evolutionary history of animals and plants?

3. Is asexual reproduction commoner in animals or in plants? Explain.

4. Why was the existence of sexual reproduction recognized much later in plants than in animals?

5. Of what disadvantage would it be to living things if heredity were absolute and all offspring resembled their parents exactly?

6. What analogy can you draw between heredity and the development of crystals?

7. Of what practical importance is the question as to whether acquired characters are inherited?

8. In the history of a science what method of investigation generally precedes that of experiment? Illustrate this evolution in method from the history of some science.

9. In general, the biological sciences have not progressed as far or as fast as the physical sciences. What explanation can you give for this fact?

10. What is the essential characteristic of the "experimental" method of investigation?

11. Animal breeding has, until recently, made much greater progress than plant breeding. Why?

12. In what way may knowledge of genetics be of value in explaining organic evolution?

13. What improvements in the human race can you think of which might be made possible by an increased knowledge and application of the principles of genetics?

REFERENCE ASSIGNMENTS

1. What are the most important ways in which living things differ from dead ones?

2. What is the physical and chemical nature of protoplasm?

3. Give an account of the "spontaneous generation" controversy waged between Pasteur and some of his contemporaries.

4. Give an example of asexual reproduction among plants and among animals.

5. What important contribution was made to our knowledge of inheritance by each of the following?

Naudin	Knight
Darwin	Focke

6. What is the history of the Cell Theory?

7. What are the main lines of evidence on which the theory of organic evolution is based?

8. What evidence is there of evolutionary development in the inorganic world?

9. Describe the work of Kölreuter and explain its importance for genetics.

10. What is the difference between *inductive* and *deductive* reasoning? Which is more generally employed in modern science? Why?

CHAPTER II

HEREDITY AND VARIATION

The chief aim of genetics is to discover, to classify, and to explain the facts of heredity and variation. Heredity is the tendency of animals and plants to resemble their ancestors and relatives; whereas variation is the tendency to depart or differ in any particular from the others of their kind. Both tendencies are familiar to all observers of man, animals, or plants. Heredity is illustrated by the remarkable resemblances which are often seen between father and son; variation by the many imperfections in this resemblance, resulting in distinct differences in their physical and mental natures. These two great tendencies, the one toward resemblance or sameness, the other toward variety or differentness, exist together in all forms of life. They are fundamental peculiarities of protoplasm which is at once so stable and tenacious of its form, and so adaptable and responsive in its reactions. Both are essential to the evolutionary progress and success of the individual and the species, just as the conservative and the radical are necessary to the advance of civilization. The one holds gains already made; the other provides the innovations which result in change and continued development. Variation, it might be said, creates new kinds of living things; heredity preserves them. In this book the entire discussion of the facts and principles of genetics will be concerned with a consideration of these two main aspects of the phenomena of inheritance, and it may, therefore, prove valuable at the start to outline briefly certain of the main features of each.

Heredity.—The remarkable resemblance between related organisms is so familiar that its significance often is not realized. When one remembers that a complex animal or plant develops from a single minute cell, it seems astonishing that the progeny should bear so close and general a resemblance to the parents. That the fig tree bears only figs and never thistles and that the progeny of horses reproduce unfailingly the general features of the horse, are not truisms, but indications of some deep-seated law or set of causes.

These resemblances may be general and common to whole groups of organisms, such as the peculiarities of men which distinguish them from other animals; or they may be specific and minute, and peculiar to a very few individuals, such as the streak of white hair or forelock which occurs in some of the members of a particular family (Fig. 6).

These resemblances between the members of groups of various sizes—races, families, or small groups of individuals—can often

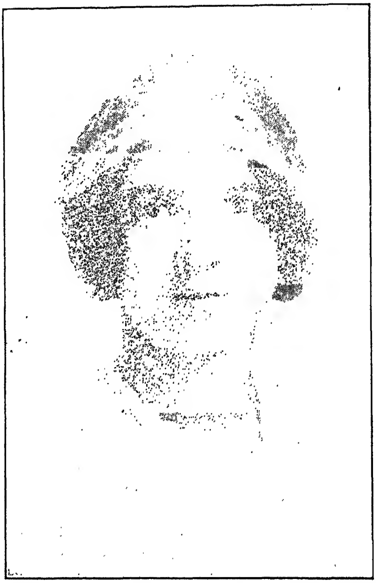


Fig. 6.—White forelock, an individual trait. (*From Miller, in Journal of Heredity.*)

be shown to be due chiefly to relationship and hence to heredity. According to the doctrine of evolution the peculiarities of large groups of organisms have arisen first in one or a few individuals from which the group has descended, and through the operation of heredity and the multiplication of the type have come to characterize larger and larger groups. As illustrations of the facts and methods of heredity, then, racial, family, and individual traits may be chosen.

Racial Traits.—It is a natural tendency to notice and remark differences rather than resemblances, and in beginning the study of heredity resemblances between the members of a group must first be considered as constituting differences between this

group and all other groups. Thus in describing a person the traits by which he differs from his fellows are specified. Upon seeing more of his fellows, it is found that the description which was thought specific applies equally well to all of his relatives. There are not only dark men and light men, but whole races of dark men and light men, as, for instance, negroes and Europeans.

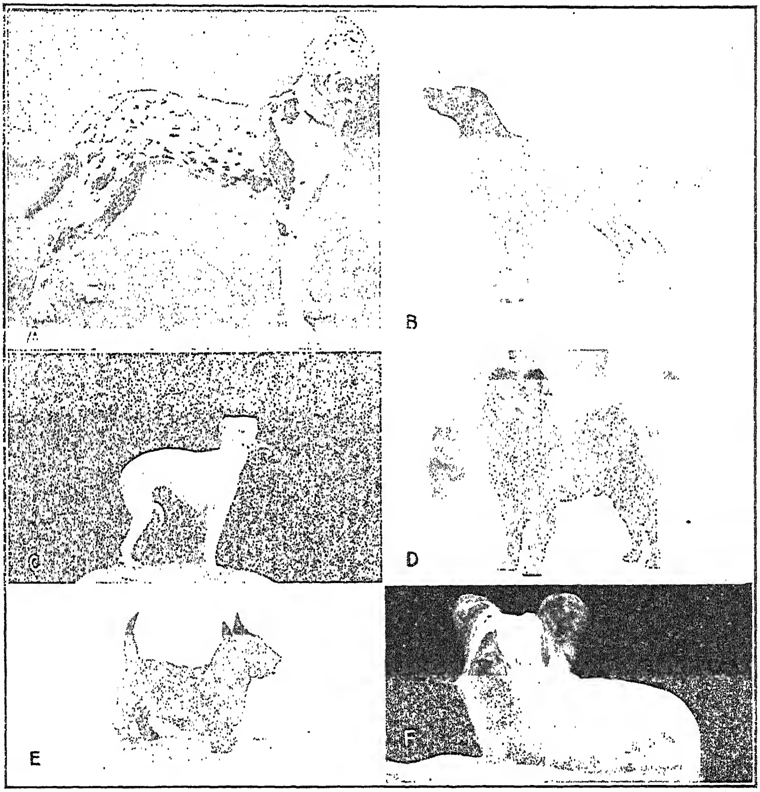


FIG. 7.—Racial variation in dogs. *A*, Great Dane; *B*, Irish Setter; *C*, Whippet; *D*, Chow; *E*, Scottish Terrier; *F*, Skye Terrier. (*Courtesy of "The Field, Illustrated."*)

The European and the negro each retains his own peculiar skin color even when both have removed to a new and common environment in America. In this case the original racial environments have been left behind, but the inheritance from white European and dark African ancestors has come to America in their descendants. The resemblances among the negroes in skin color and

their differences from the white races are thus seen to be due not to the differing environments in which they live, but to some innate or hereditary difference. Whatever its cause, this presumably arose in one or a few ancestors of the present negro peoples, and has been transmitted to all of their descendants.

The hereditary nature of many racial traits among our domesticated animals has long been recognized by breeders and accounts for the careful pedigrees which have been kept for many races or breeds of livestock (Fig. 7). The importance which the Arabs attributed to inheritance in producing the characters which they desired in their horses is evidenced in their laboriously kept pedigree records and their insistance that no horse could be regarded as a typical or purebred Arab which did not trace its ancestry to one of five noted animals which became the parents of the Arab breed. The similarities and uniformity of the progeny, they recognized, were due to descent rather than to the locality of birth.

Among plants such racial traits received tardier recognition, and the importance of ancestry and pedigree has only recently been emphasized. Now that the processes of reproduction are known, matings may be controlled in plants as well as in animals, and many distinct races of cultivated plants have been bred. Kanred wheat, which now covers a large portion of the wheat acreage of the western United States, is a strain possessing certain traits which make it superior to all other varieties for these regions. Its value lies in the resemblance of all of the present members of the Kanred variety to a few ancestors which possessed these desirable traits.

Family Traits.—Although family traits have been distinguished from racial, no sharp line can be drawn between them, for traits which at one time may characterize close relatives, may with the increase of the family in numbers become common to a much larger group. Among men and other animals certain families appear to be distinguished from others of the same race by noticeable physical and mental peculiarities. It is well known that there are hereditarily able families and hereditarily incompetent families, and occasionally the difference between the able and the incompetent may be traced directly to a difference in descent. Such is the case in two human families in America. The descendants of Jonathan Edwards have included men and women eminent in every field of American life, yet the grandfather of

Jonathan Edwards also became the ancestor, through a second marriage, of a line quite unremarkable for achievement.

The same sort of family resemblances and differences exist within a single breed or race of domesticated animals and plants. Among dairy cattle, where the production of milk and butter fat is the chief criterion, famous milk families such as the May Rose family of Guernsey cattle and many others have arisen in the principal breeds, all tracing descent from one or a few ancestors which were themselves remarkable either as milk producers (Fig. 8), or, in the case of the male ancestors, as sires of high-

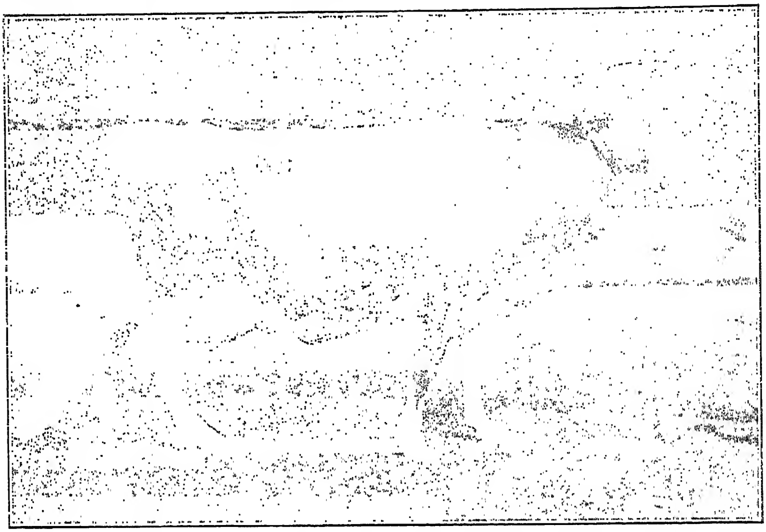


Fig. 8.—A notable progenitor. May Rose II, a Guernsey cow famous as the founder of a family of superior animals which has developed into the May Rose-line in the Guernsey breed. (*Courtesy of the American Guernsey Cattle Club.*)

producing cows. Among trotting horses where the desire for speed rules the breeding and training methods, the fastest horses and the parents of the largest number of superior offspring have nearly all belonged to the family founded by the famous Hambletonian 10.

Individual Traits.—Aside from illustrating the universality and importance of heredity in determining the racial and family features of plants, animals, and man, the above examples lead us no nearer to an understanding of inheritance. It is interesting and valuable to learn that such traits as the skin colors of men, the quality of wheat, and the speed of horses are inherited; but

it is more important to know how this remarkable force of heredity works. In order to do this some instance must be chosen of a single specific trait which may be observed in several generations of *individuals* whose descent and relationship are known. The trait thus chosen does not necessarily differ in any important respect from those distinctive of race or family as mentioned above, and its inheritance is typical of the laws which probably govern the inheritance of these more complex traits. Eye color in man may happen to be a character which distinguishes one individual from another but it may be one item in a racial description as well. Thus anthropologists say that a racial group of northern Europe—the Nordic type—is, in general, blue-eyed; while the southern European (Mediterranean) type is prevailingly brown- or dark-eyed. The particular interest for genetics lies in the presence of blue or brown eyes in single related individuals.

Unit Characters and Factors.—Investigation shows that marriages of blue-eyed persons with brown-eyed ones from a prevailingly brown-eyed family, produce exclusively brown- or dark-eyed children. When these children marry other brown-eyed children of similar ancestry, (that is, having one blue- and one brown-eyed parent), *their* children are found to resemble the brown-eyed grandparent in a large proportion (about three-fourths) of the cases, while the remainder, about one-fourth, are blue-eyed Thus each grandparental type reappears in a definite proportion of the grandchildren. The regularity with which such a result is obtained and the distinctness with which traits like blue and brown eyes are assorted to different individuals among the progeny have led to a definite conception of the mechanism of heredity which will be more fully described in the next chapter. It should be pointed out here, however, that blue eyes appear to pass as a *unit* to one group of progeny, while brown eyes pass as a *unit* to another group, and since the only mode of hereditary transmission is through the reproductive cells or gametes of the parents, it may be assumed that the gametes of the parents differ in respect to something which represents or determines the development of eye color in the progeny. This something which appears to pass through the reproductive cells and to influence a particular character in the offspring is known as a *factor*, *unit factor*, or *gene*. The *character* "brown eyes" in the child or adult, therefore, is ascribed to a *factor* for brown

eyes in the reproductive cells which gave rise to the child; and thence to the gametes of the parents and more distant ancestors. The reproductive cells or gametes appear to contain factors representing all of the inherited characters of the animal or plant; and the organism from this point of view is a complex mosaic of a vast number of inherited units which in every generation pass through the single reproductive cells of each parent and find expression in the various traits of the offspring (Fig. 9). The factor hypothesis, which has been amply verified by data from all forms of life, has led to the discovery of the laws governing the behavior of these units in heredity.

FIG. 9.—Black and white, a unit character difference in rabbits. (*From Castle.*)

Complexities of the Factor Hypothesis.—In the inheritance of blue and dark eyes in man, a single factor appeared to be responsible for the difference. It must not be concluded from this that any character of the organism is completely determined by a single factor or by inheritance alone. Complete analysis generally shows that many factors, which may not always be entirely separable in their inheritance, are involved in the production of characters which appear to be quite simple, and that the expression of these factors in development is influenced by many agencies both within the organism and in its environment. The gray or grizzled pattern of many wild rodents, such as mice and rats, appears to be a simple trait, yet its development depends on the interaction of at least a dozen different factors affecting the various colors involved and their distribution in the fur. Many characters, such as horns in some breeds of sheep, are determined by a single factor, but their expression is greatly influenced by the sex of the individual; while in other cases, for example in the inheritance of color blindness in man, the inherited factor itself is constantly associated with the factors which determine the sex of the individual. Other internal agencies.

such as hormones or the secretions of the ductless glands, are known to affect profoundly the expression of the genetic factors.

What Is Inherited.—It is known that many characteristics of the organism are also dependent on the environment in which it lives. In the corn plant a large number of inherited differences in plant colors have been found, in addition to the normal green. When one of these varieties, known as Sunred, is grown in the field, a red color appears in the leaves, in the outer husks of the ear, and in other parts which are exposed to the sunlight (Fig. 10). When these parts are protected from sunlight, however, no red pigment develops. The Sunred condition is inherited, and when corn possessing the factor for it is crossed with a

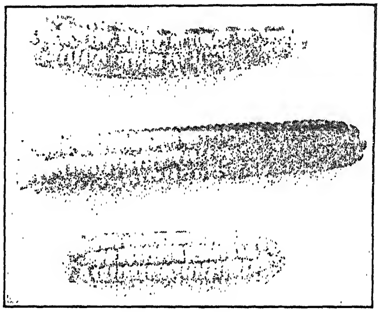


Fig. 10.—"Sunred" corn. The ear at the bottom had been protected from light and the one in the middle exposed to light at its tip, which turned red. In the ear at the top the word "LIGH(T)" was cut out of the husks and the area thus exposed turned red. (*From Blakeslee, in Journal of Heredity.*)

green variety, a portion of the second generation plants become red if exposed to sunlight. Sunlight, an environmental factor, is needed in order to distinguish between the Sunred and green plants. These red plants have not inherited a character "red," but only the ability to react to an external condition (sunlight) differently from their green relatives.

Instances of the same sort of reaction may be drawn from animals. Some species are known to have an hereditary immunity to certain diseases or parasites, as in the case of the zebu, which is much more resistant than our American breeds of cattle to Texas fever and the tick which carries the disease. Among mice it has been shown that a single factor may differentiate a race in which a transplantable tumor will grow, from one in which the tumor will not grow. In all these cases it is plain that what is inherited is a peculiar or unique potentiality for

response to a particular set of conditions both within and without the organism.

Diversity of Inheritance.—The few examples of heredity which have been given are instances chosen from thousands of traits in man, animals, and plants. Data have been gathered and the mode of inheritance described for such diverse characters as feeble-mindedness in man, coat colors in horses, cattle, and dogs; the habit or gait of animals, such as trotting in horses or the peculiar waltzing of some varieties of mice; the length of life of flies; the probability of death from certain causes in a number of animals; the time of flowering; the shape, size, and number of flowers and fruits in plants; and many others. The kind of trait apparently has no relation to the method of inheritance, since all types are subject to inheritance and appear to be governed by the same rules or laws. All are referable to certain hypothetical factors in the germ cells which connect one generation with the next. These factors appear now to be the actual units of inheritance and of living matter, just as the atom may be regarded as the unit of matter in the chemical or physical sense. These units are dependent on one another and on both the internal and external environment of the organism. In combination with all these they determine the characters of living things. Much of the study of inheritance and of variation must, therefore, be intimately concerned with their origin, changes, effects, and mode of inheritance in living plants and animals.

These examples indicate that heredity is operative everywhere and that throughout the organic world there is a constant tendency for offspring to resemble their parents. They also show that heredity is not a simple process, uniform in its operation and definitely predictable in its results, but that different characters, even in the same individual, are inherited in different ways. To classify this host of diverse and often seemingly contradictory facts and to discover the general laws which underlie them is the province of the student of heredity, and although a notable beginning has been made at this task, we must admit that many of the phenomena of inheritance are still unexplained and unpredictable.

Variation.—If one now turns to the other side of the picture and examines these same facts but notes especially the variations rather than the resemblances between individuals, he should real-

ize that he is not encountering a new subject but is only looking at the phenomena or inheritance from a somewhat different point of view. Variations, like resemblances, are not all simple and similar but are remarkably diverse in cause and in character (Figs. 11 and 12). Among these variations, however, careful study is able to discover several very distinct types, which resemble each other in appearance but are totally different in their underlying causes. Indeed, it is one of the first cares of a geneticist to recognize these different kinds of variations and to learn to distinguish carefully those which are of significance to

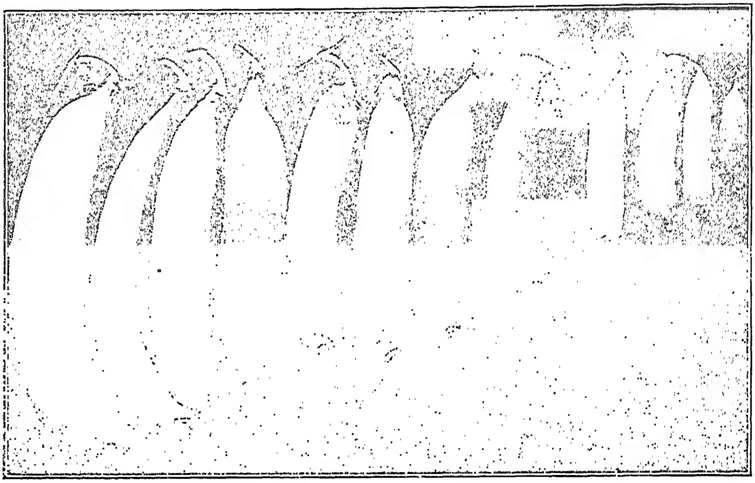


FIG. 11.—Variation in size, shape and color in pods of different races of peas. (*From O. E. White.*)

him from those which are not. A few characteristic examples of variation will perhaps serve to make these points clear.

Due to Environment.—Among Chinese primroses there is a race which produces *white* flowers if grown at a relatively low temperature and *red* flowers if grown at a relatively high one. This variation in flower color within a perfectly pure race of plants is evidently due entirely to differences in the *environment* in which the plants are growing rather than to variation in the genetic make-up of the plants themselves. There are other races within the same species of primrose, however, which will produce nothing but white flowers, regardless of the conditions under which they are grown, and still others which will breed perfectly true to red. The difference between red and white in

—Variation in the head appendages of male fowls. Each form is typical of a pure breed or variety of domestic fowls. (*From Robinson.*)

these latter cases, unlike that which we first mentioned, is therefore clearly not due to the environment but to a difference within the plant itself.

Characters of size or quantity, as opposed to those of quality alone, are notoriously variable, and in many cases these variations are clearly due to environmental causes. It is easy to observe the remarkable differences in height, number of leaves, yield of fruit and other quantitative characters which exist between plants grown in poor soil and others of precisely the

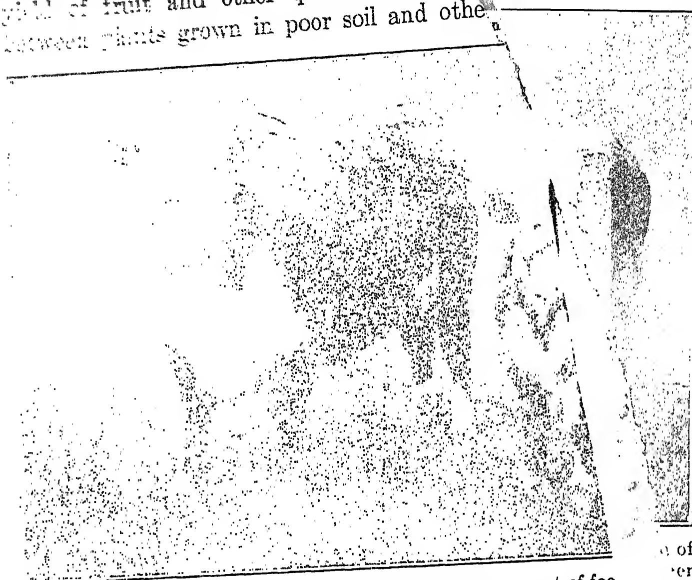


FIG. 13.—Variation in size caused by differences in amount of foo[d] these animals is two years old. The one at the left was fed liberal[ly] sparingly. (From Jones, after Mumford, Courtesy of John Wiley a[nd Sons].)

same variety which are grown in rich soil. Among the same way, the quality and quantity of food de[termine] a very considerable degree many size characters. ration which is fed to a steer (Fig. 13), a cow, or a h[en] great deal of difference in the number of pounds of be[ef], milk, or dozens of eggs which are produced. So po[tent is the] effect of the environment on characters of this so[rt] (obviously very important ones economically) tha[t] agricultural practices are concerned with such a ma[nipulation of] the environment—whether of fertilizers, water, food, or other factors—that the most desirable va[riations may] be induced.

Due to Hybridization.—Many variations, however, are due not primarily to the environment but to a reappearance or recombina-

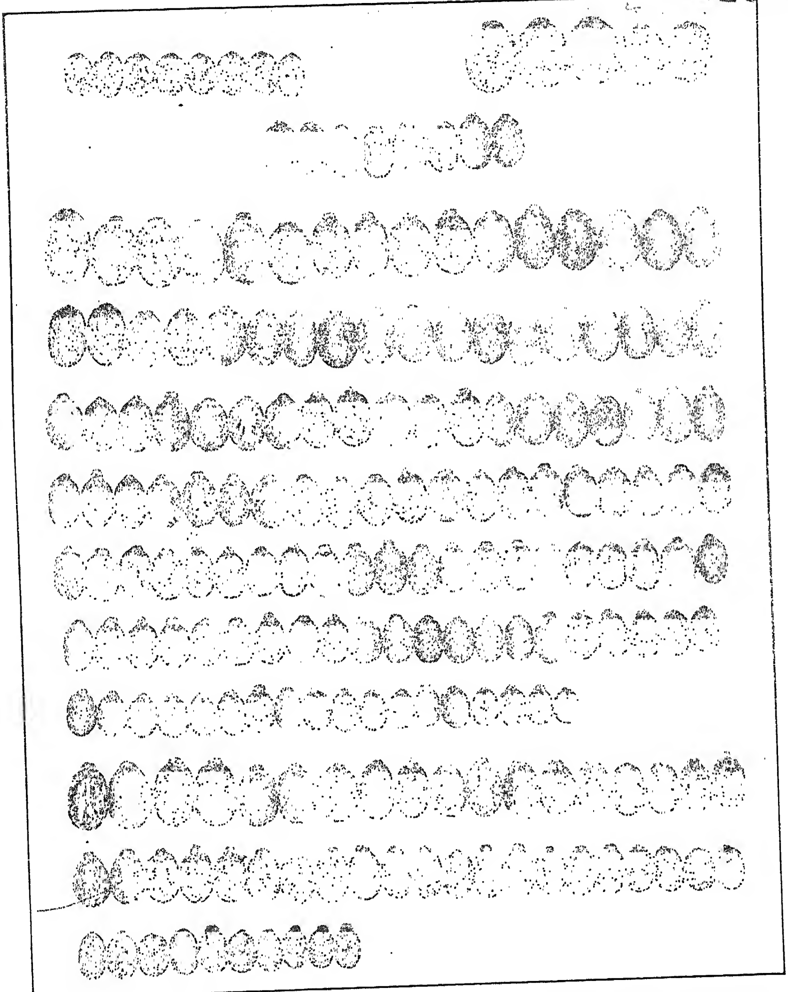


FIG. 14.—Variation in size, shape, color and mottling in castor beans, following hybridization. The two parental types, at top, and the first generation, below them; followed by one seed of each plant of the second generation. (*From White, in Journal of Heredity.*)

tion of hereditary traits among the descendants of individuals of mixed or impure genetic constitution. It has already been seen that, in man, the mating of a blue-eyed individual with a (pure)

brown-eyed one will produce a hybrid generation which is uniform, but that among the grandchildren both brown-eyed and blue-eyed individuals appear, and in very definite proportions. Such variation is due to the sorting out of genetic factors in the generations following a cross (Fig. 14).

Where the individuals which are crossed differ in only a single character, but little variation (in this case only the presence of brown eyes and blue) occurs among the offspring. Where a cross brings together individuals unlike in several characteristics, however, variation is markedly greater, for the number of possible combinations of traits will increase. If two pairs of characters are involved, for example, there will be four possible combinations among the descendants; if three, there will be eight; if four, sixteen, and so on. $2c_1 \times 2c_1 \times 2c_1 = 8$

Size or quantitative characters, in so far as they are inheritable, also show this increased variability following a cross. If a genetically large animal is crossed with a genetically small one, for example, the first generation offspring are often intermediate in height, and uniform, but *their* descendants are generally highly variable, ranging all the way from tall to short. There is reason to believe that this increase in variability is also due to a recombination of genetic factors, although here the factors all affect the same character of the animal, its size.

This increase in variability which always follows hybridization between unlike individuals has resulted in the appearance of many new character combinations in animals and plants, and has made it possible for breeders, by practising selection among these, to develop new and valuable types. It also accounts for the well-known fact that hybrids or mongrels, whatever their own excellent qualities, do not breed true and hence are valueless for breeding purposes where uniformity of type is desired.

Due to Mutation.—Variations due to the environment can be controlled by a proper manipulation of the environment itself, and variations due to the sorting out and rearrangement of factors can also be controlled through a knowledge of the laws which govern the behavior of these factors. There is a third type, however, which it is as yet impossible to predict and over which there is no control. If a breeder follows carefully a group of animals or plants from generation to generation, he will occasionally find an individual recognizably different from the rest of the population and breeding true, but the origin of which he

cannot explain by anything in the environment or in the past history of the race. Such a variation is known as a *mutation*.

In the history of plant and animal breeding occur many instances of such sudden variations. In the latter part of the eighteenth century, for example, there appeared in the flock of Seth Wright, a New England farmer, a male lamb with remarkably short, bowed legs. Wright reared this lamb and bred from it,

FIG. 15.—The Shirley poppy, which originated as a mutation from the wild field poppy.

thereby originating the Ancon breed of sheep, so short-legged that they could not jump over an ordinary stone wall. In the same way hornless mutant individuals have appeared in almost all breeds of horned cattle, and hornless races of these breeds have been developed from them. Pacing horses, double-toed cats, "mule-footed" swine, albino rats, and many other new, distinct, and true-breeding types have appeared as mutations among animals.

Nor have plants been less subject to this form of variation. In 1880, the Rev. W. Wilks, Vicar of Shirley, England, discovered

in his garden an individual plant of the ordinary wild field poppy which was markedly unusual, and from seed saved from his plant has arisen the Shirley poppy as it is known today (Fig. 15). The dwarf "Cupid" sweet pea, now extensively cultivated, has come from a single plant appearing in a seedsman's garden. In the same way the purple beech, Stewart Cuban tobacco, rainbow corn, and cut-leaved, double-flowered, and white-flowered races of many plants have sprung suddenly into being, bred true, and founded new and distinct races.

Most of these mutations in plants arose from seed, but in some instances the mutant character was found to be confined to a single branch. Such a branch, when artificially propagated, remains true to its new type. Many horticultural varieties, especially those with variegated foliage, have arisen from such mutations or "bud sports."

Early students of mutation emphasized the wide divergence of mutating forms from the normal type, but it is now recognized that mutational differences may be large or very small, and that it is not their size but their clear distinction from the parent form and their ability to breed true to the new type which distinguish them from other kinds of variation. In many cases, indeed, it is very difficult to tell whether one is dealing with a mutation or with a complicated case of the sorting out of genetic factors.

Variations may therefore be divided into three main groups: (1) those which are due to differences in the environment; (2) those which are due to reappearance and recombination of genetic factors; and (3) mutations, the cause and origin of which we do not understand. The first of these is of little importance to the geneticist, except that he must learn to distinguish it from the others. The second, however, is of the greatest significance to him, because here alone he can control changes in type. The third is of value in providing him with new and heritable forms with which he can work, although his skill is here employed, as yet, only in detecting rather than in predicting or controlling them.

QUESTIONS FOR THOUGHT AND DISCUSSION

14. Why do you think it was that, although plants and animals had been bred for thousands of years, the fundamental laws of inheritance were discovered until very recently?

15. Why have pedigrees been kept much more carefully for our domestic animals than for our cultivated plants?

16. If "the peculiarities of large groups of organisms have arisen first in one or a few individuals from which the group has descended," why is it that living members of the two groups today—a sheep and a goat, for example, or an apple tree and a pear tree—cannot be successfully crossed?

17. What other family beside that of Jonathan Edwards do you know of which has included a large number of eminent people?

18. The eyes of all brown-eyed people (or of blue-eyed ones) are not alike but differ considerably in shade, pattern, and other features. To what do you think these differences may be due?

19. In what way could our knowledge of the inheritance of eye color in man be used to decide a case of disputed paternity?

20. What mechanism, either physical or chemical, can you imagine whereby a *factor* in a gamete might determine the appearance of a *character* in the individual produced by that gamete?

21. Does an organism ordinarily display all the traits for which there were factors in the gametes which produced it? Explain.

22. Some races of Teazel have spirally twisted stalks if grown in rich soil but normal straight ones if grown in poor soil. How does a normal plant from such a race differ genetically from a normal plant of a race which never shows twisting?

23. The hair color of an individual may be brown in youth, black at maturity, and white in old age. What color would you call his hair in a study of inheritance of hair color in his family? In investigating the inheritance of hair color, what precaution, therefore, should be exercised?

24. What environmental agency is necessary to distinguish a disease-resistant race of plants from one which is not?

25. How could you determine whether a given case of variation is due to environmental or genetic influences?

26. In general, are qualitative or quantitative traits more susceptible to environmental influences? How do you account for this?

27. Why is it more difficult to study the inheritance of such characters as size and yield than of color?

28. How can you tell whether a new trait is a mutation or the result of complex segregation following a cross?

29. Do you think that variations due to inborn genetic differences, or to the environment and training, are the more important in determining differences between persons?

30. What explanation have you for the present great variability of the human race? Why would you expect the population of the United States to be more variable than that of most European countries?

31. How are individual variations utilized in the identification of persons?

REFERENCE ASSIGNMENTS

11. Name a race of cultivated plants (other than the one mentioned in your text) which has recently been developed by breeding and which is particularly successful.

12. Give an example of a human family pedigree showing the inheritance of mental or physical defects.

13. Why is color blindness more common in men than in women?

14. Look up and explain a case of "reversion."

15. Give an example, aside from those mentioned, of a trait which behaves in inheritance like "Sunred" corn, requiring the presence of a specific environmental agency for its expression.

16. It is sometimes maintained that the "social" inheritance of an individual is of more importance in determining his traits than is his "biological" inheritance. What does this mean?

17. Give an example of variation which is clearly due to segregation of genetic factors.

18. Name some examples aside from those mentioned in the text, of new plant and animal types which have arisen by mutation.

CHAPTER III

MENDEL'S LAWS OF INHERITANCE. I

The facts discussed in the previous chapter make it very evident that the problem of inheritance, far from being a simple and clearly defined one, involves a whole series of problems touching many fields. Different characters are inherited in very different ways, and variations may be due to all sorts of causes. Knowledge derived from a study of one species is often useless in the case of another. When the great assemblage of diverse and often seemingly unintelligible facts which students of inheritance are amassing is considered, it is not surprising that earlier biologists were long unable to reduce them to an orderly and understandable basis.

No branch of knowledge, however, is entitled to be called a science until its various facts can be arranged and classified under certain definite principles or *laws*, a knowledge of which makes it possible to understand these facts, at least in part, and to predict or control them. The conception of scientific law is so important and often so poorly understood that it may be profitable to digress a little here and to consider briefly what a law of science is and how it may be discovered and applied.

The Laws of Science.—The external world is continually presenting to the senses a multitude of diverse objects, the character and relationships of which cannot be discerned by observation. Many of these phenomena appear at first sight to be irregular and unpredictable and to have no definite relationship to one another. It is soon noted, however, that running through this apparent confusion there are indications of regularity and order and that some events follow others so invariably that one may confidently depend upon their always doing so. The observer thus learns to distinguish the relationships known as *cause* and *effect*. The constant association between the position of the moon and the height of the tides, or between the length of a pendulum and the rate of its oscillation, are examples of such evident uniformities. This conception of *orderliness* in nature

grows upon the student as he acquires more facts and studies them more critically, and he soon realizes how useful a recognition of this orderliness may be in foreseeing events and in directing their course.

That the universe is indeed fundamentally orderly and that more complete knowledge will make it possible in time to perceive this order in all things is the faith of every scientist. To the constant relationships in nature which he is learning to recognize in ever-growing numbers he has given the name of *laws;* and the chief purpose of scientific investigation is to extend existing knowledge of these laws over a wider and wider field until all facts which now seem confused and irregular shall take their places in an orderly system.

The formulation of a scientific law is by no means an easy matter, however, and has often required an exercise of supreme genius. An attempt to establish such a law involves several distinct and well-recognized steps. First, as much information or data as possible concerning the phenomena under investigation must be gathered. This may be done by direct observation under natural conditions, but a more fruitful procedure, and one employed wherever possible, involves a control of conditions by the observer himself so that a definite *test* may be performed. This method is known as an experiment, and since it makes it possible for us to single out a particular group of phenomena and test their behavior at will under conditions which are known and can be regulated, it provides more exact information than can be gained in any other way, an advantage which has made the experimental method one of the most useful tools of modern science. The information thus gained, which is often somewhat unintelligible at first sight, must then be arranged and classified. If this classification is wisely made, the discerning eye may perhaps begin to see certain simple relationships which underlie the facts, and eventually a tentative explanation or *hypothesis* may be framed to account for these observed relationships. The hypothesis is then thoroughly tested by further observation and experiment, and if it continues to explain satisfactorily all the facts which are brought forward, it leaves the realm of conjecture and becomes accepted as an established scientific law. A law is thus a brief statement or explanation of some uniform and constant relationship which has been found to hold through a large series of natural events.

Mendel and His Methods.—Mendel's discovery of these first laws of inheritance led through precisely the steps of observation and experiment, classification, tentative explanation or hypothesis, testing, and final deduction which have been outlined above. The most important facts in the life and work of this Austrian monk whose name has become woven so closely into the fabric of genetic science have already been presented. In the garden of his monastery at Brünn, Mendel began in 1857 to observe carefully the resemblances and differences among various races of garden peas. It is perhaps noteworthy that he was not a professional biologist but that these experiments were his chief avocation, stimulated by a natural curiosity which he had the leisure to indulge.

Mendel was prepared for his work by a fine enthusiasm and a thoroughly scientific spirit, and was also familiar with the results of earlier investigators on the subject which most interested him, the effect of crossing or hybridization on plants. His success was due not only to these qualities of mind but also to a wise choice of materials and methods of investigation.

Counting of Different Types of Offspring.—Mendel endeavored to get away from the complexities which had troubled earlier students of heredity by simplifying the problem as far as possible. Many workers had noticed that when plants of different varieties were crossed, great variability appeared among the progeny of the hybrids, as had always been apparent from the results of breeding mongrel animals. No one, however, had been able to simplify these confused and puzzling observations until Mendel brought to their solution a new and effective method. This consisted in actually *counting* the *numbers of each type of progeny* which resulted from a given cross, in grouping them into definite and easily recognized classes and in observing the relative sizes which these classes displayed. He thus for the first time began to reduce the phenomena of inheritance to a *measurable* basis and employed the exact quantitative methods used so successfully in many other sciences. Herein lay one of Mendel's chief contributions to genetic discipline.

Study of Single Traits.—Where earlier investigators had made general observations upon the animal or plant as a whole, studying at once the great variety of traits and structures transmitted to each by inheritance, Mendel instead still further simplified the problem by confining his attention to a single character at

a time (Fig. 16). In studying flower color, for example, he chose for his hybridization experiments plants which were contrasted in this one character alone, crossing a red-flowered plant with a white-flowered one, and paying no attention for the time being to whether these plants were tall or dwarf, yellow-seeded or green. When the behavior of each single trait was established, he then studied two traits together, such as flower color and vine

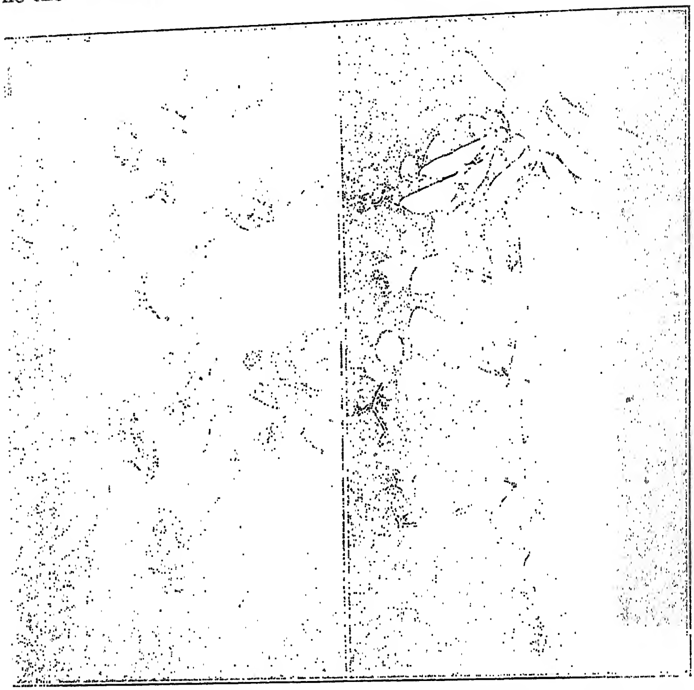


FIG. 16.—One of the pairs of character differences studied by Mendel in peas. At left, flowers and pods axillary, borne along the stem; at right, flowers and pods terminal and stem somewhat flattened. (*From O. E. White.*)

height, and thus extended his analysis still further. By attacking the problem bit by bit he at last succeeded in discovering order and regularity where his predecessors had been able to see only confusion.

Pedigree Records.—In tracing these characteristics from generation to generation a careful technique and a thorough system of recording observations became necessary, since it was of the utmost importance to know exactly which plants were the parents of each individual, or the offspring of a given cross. This

involved the task of keeping full and precise pedigree records of all plants studied, including the identification of each by a number or symbol, an exact statement of its parentage, and a complete description of its various traits in so far as they concerned the problems under investigation.

These innovations of Mendel's—counting the different types of offspring, studying single characteristics independently of the whole individual, and keeping accurate pedigree records of the members of successive generations—are simple enough in themselves, but such a thorough application of the experimental method to breeding problems had never been made by any other investigator. The important discoveries which Mendel made were largely due to these new methods, and they have since been the basis of all careful genetic research.

Material and Technique.—Mendel also chose his material wisely and adapted his technique to conform to the objects which he had in mind. The garden pea is a naturally self-fertilized species. Its flowers are so constructed that the reproductive parts are covered by the petals and not exposed to insects or the wind Pollen normally falls on the adjacent stigma and thus effects fertilization of the ovules of the same flower. Only in rare cases do insects penetrate the flowers, so that there is ordinarily no cross-pollination between plant and plant except as it may be artificially effected by the experimenter. Mendel could, therefore, open a flower bud and remove the stamens before any pollen had been shed (thus preventing self-pollination), and later place on the stigma of this flower, pollen from the plant which he wished to use as the other parent in a cross. It was, of course, necessary to guard this artificially fertilized flower against contamination by pollen of unknown origin which might be brought thither by wind, insects, hands, or instruments. If he wished to determine the kind of progeny which would appear in the second hybrid generation following a cross, he therefore had only to allow the flowers of these plants to fertilize themselves naturally. The pea had the further advantage of being available in a large number of well-marked varieties which bred true and were all fertile when crossed with one another. In some of these, as in the varieties offered by seedsmen today, the plants were tall and regularly attained a height of six feet or more, whereas others were low and dwarf. Some varieties had yellow seed and others green; some had round seeds

and others wrinkled ones; some had colored flowers and others white; and there were a number of other readily distinguishable differences. In several particulars, therefore, the pea was more satisfactory material with which to work than most other plants would have been.

Mendel's procedure was to cross two plants differing in one of these contrasted character-pairs, to plant the seed thus obtained, and to observe the appearance of the first hybrid or "F_1"[1] generation. He then crossed two hybrid plants together (or allowed them to effect self-fertilization) and raised as large a number as possible of second generation or F_2 offspring. These were found to display more or less variation in the character studied and he accordingly classified them, counting the number of plants possessing each of the contrasted traits. Mendel not only crossed plants differing in one trait but later made hybridizations involving two character differences and observed their behavior in the first and second hybrid generations.

From a study of such comparatively simple data were formulated hypotheses which have since been so widely verified by experiments with many other plants and animals that they are now clearly established as Mendel's Laws of Inheritance. These include several distinct principles each of which will be considered by itself and illustrated by typical examples from the experiments of Mendel and of later investigators.

The Principle of Dominance.—One of the first facts brought out by Mendel's experiments was that the two members of a given pair of contrasting characters, when brought together in a cross, differ markedly in their ability to express themselves in the resulting hybrid offspring. When he crossed a pure-breeding red-flowered plant with a pure-breeding white-flowered one, for example, the progeny were found to resemble exactly the red-flowered parent (Fig. 17). No white-flowered plants and no intermediates appeared. He knew that whiteness had not really been eliminated, for in the subsequent generation white-flowered plants cropped out again; but in the hybrid itself whiteness seemed to be suppressed or to recede from view and redness to dominate. Mendel therefore called such a trait as redness of flowers a *dominant* one and such a trait as whiteness a *recessive*

[1] The parental generation is technically known as the P_1, the first generation following a cross as the F_1 (first filial generation), the second as the F_2, and so on.

one. All of the seven characters in peas reported by Mendel behaved in this way, one of each pair of contrasting traits appearing to be dominant and the other recessive. Thus the round form of seed was found to be dominant over the wrinkled; the yellow color of the cotyledons over the green; the inflated form of pod over the constricted; the green color of the unripe pods over the yellow; the axillary position of the flowers and pods over the terminal, and the tall vine habit over the dwarf.

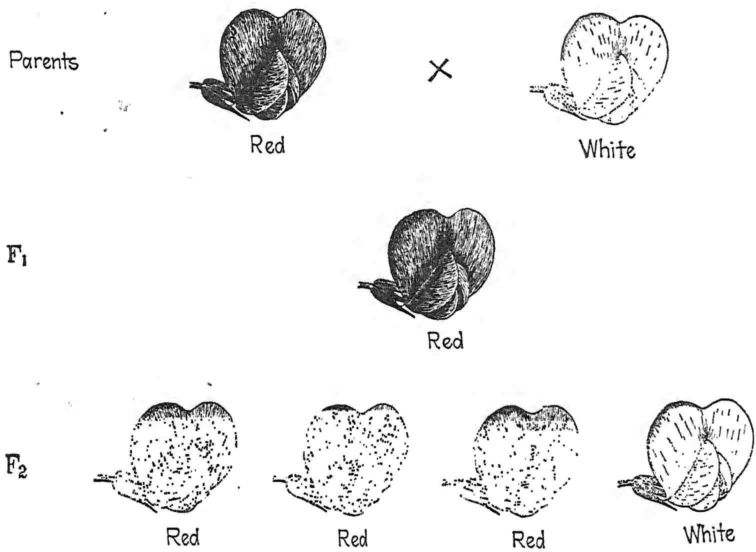


FIG. 17.—Cross between a pure red-flowered and a white-flowered pea plant, showing the dominance of red flower color in F_1. If an F_1 plant is self-fertilized the resulting F_2 generation is three-fourths red-flowered and one-fourth white. or when two of them were crossed.

In all these cases the dominance of one character over the other was essentially complete. Mendel emphasized this fact, and later investigators have found many characters which show similarly complete or practically complete dominance. In very many other cases, however—and their number grows as the knowledge of inheritance in plants and animals becomes greater—dominance is absent and the hybrid individuals resemble neither parent exactly but are more or less intermediate between the two. In the snapdragon, for example, a crimson plant crossed with a white one gives first-generation hybrids which are all *pink* in flower color (Fig. 18). In the same way a black Andalusian fowl bred with a splashed white one produces offspring

which are "blue" in the color of their plumage (Fig. 32, p. 86); and in Shorthorn cattle the cross of red coat and white gives offspring which are "roan," their coats consisting of a mixture of red and white hairs (Fig. 19). In other instances the hybrid offspring may resemble one parent much more closely than they do the other but may not resemble it exactly, so that dominance is only partial. There may thus be all stages between complete dominance and the absence of dominance; and these various

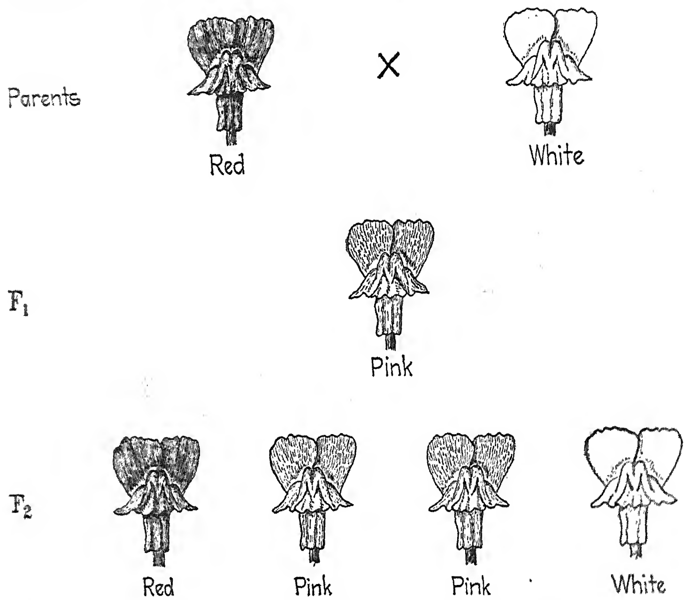


FIG. 18.—Cross between a red-flowered and white-flowered snapdragon showing absence of dominance in F_1. If an F_1 plant is self-fertilized the resulting F_2 generation is one-fourth red, one-half pink and one-fourth white.

conditions may all be found among the different traits of a single individual.

That the seven characters thoroughly studied by Mendel happened to show the phenomenon of complete dominance undoubtedly aided him in perceiving the more essential features of inheritance, but we do not now attach the same importance to this principle as did Mendel himself. A recognition of it, however, was and is important in several respects. Earlier breeders had naturally taken it for granted that the *appearance* of an individual was a sure indication of its genetic constitution and the way in which it would breed. Mendel's work has shown

that this is not necessarily true but that dominance, partial or complete, may enable a hybrid or mongrel to masquerade as a purebred individual. This fact is not only of theoretical interest but is of great importance in the practical breeding of animals and plants.

FIG. 19.—A red roan Shorthorn bull. Roan is the expression of the heterozygous condition of factors for red and for white. Like the blue of Andalusian fowls, it does not breed true. (*From Wright, in Journal of Heredity.*)

The Principle of Unit Characters and Factors.—As before noted, Mendel carried his experiments beyond the first hybrid generation and grew a second one by crossing together (or by self-fertilizing) plants of the F_1 generation. Sometimes a third and a fourth were also successively studied. The most notable feature of the F_2 raised from the cross of red-flowered with white-flowered plants was that, instead of being uniformly red like the F_1, this generation included both red and white individuals (Fig. 17). These plants resembled exactly the red and white grandparents, and no other kinds of plants appeared. In succeeding generations these same two types of flower color maintained their individuality and independence. A similar result was obtained in the second generation bred from the hybrids between other pairs of contrasted characters (Table I). These facts all vindicated the soundness of Mendel's method in studying inheritance character by character, for they showed that the traits which

differentiated these various types of peas from one another were essentially independent things which did not lose their identity in the hybrid but were passed on unchanged to the second and later generations. This independence was still further emphasized by the results of experiments (to be described later) in which individuals differing in more than one trait were crossed. Such a conception of the individual as an aggregation of more or less independent and separable "unit characters," each of which is distinct and may exist with any combination of others, was an entirely new one, but it has been fully supported by all later work and its fundamental importance is now recognized.

TABLE I.—SUMMARY OF F_2 RESULTS OF MENDEL'S EXPERIMENTS WITH PEAS

Character	Dominants	Recessives	Total
	No. %	No %	
Form of seed	5,474 (74.74)	1,850 (25.26)	7,324
Color of cotyledons	6,022 (75.06)	2,001 (24.94)	8,023
Color of seed coats	705 (75.90)	224 (24.10)	929
Form of pod	882 (74.68)	299 (25.32)	1,181
Color of pod	428 (73.79)	152 (26.21)	580
Position of flowers	651 (75.87)	207 (24.13)	858
Length of stem	787 (73.96)	277 (26.04)	1,064
	14,949 (74.90)	5,010 (25.10)	19,959

Mendel soon observed that for each of these various traits there was to be found a contrasting trait, such as red flower color with white, yellow seed coat with green, tall vine with dwarf, and so on. These pairs of contrasting unit characters which he brought together in his hybrids Mendel called "differentiating characters." The occurrence of such a paired condition in practically all characteristics of plants and animals is abundantly supported by all the available evidence. Such pairs of characters were later termed *allelomorphic* pairs, each of the two members being the *allelomorph* of the other.

In Mendel's own paper and in much of the early work of his successors, no sharp distinction was drawn between the actual and visible trait or character and that "something" which exists in the gametes and which ultimately causes the development of this character in the individual resulting from their

union. The actual character which is seen, such as red flower color, for example, obviously cannot be present in the gametes, but something representing it and capable of producing it must be there. This is called the *factor or gene* for the character in question. An important result of later mendelian investigation is a recognition that the very same factor may, under different environmental conditions, give rise to characters which are also markedly different. The constant and unchanging thing, therefore, is the factor itself rather than the character, and the unity which Mendel observed also lies rather in this underlying factor than in the visible, and perhaps variable, character which it produces. Geneticists today are careful to distinguish between the two.

The Principle of Segregation.—The behavior of these units in the second and later generations from a cross led to the discovery by Mendel of one of the most fundamental principles which govern the transmission of characteristics from generation to generation. It has been seen that when he crossed a pure-breeding red-flowered plant with a white-flowered one, the offspring were all red-flowered; and that when one of these red-flowered offspring was self-fertilized (or when two of them were crossed) the resulting second-generation plants consisted of both red-flowered and white-flowered individuals. The two contrasted characters (allelomorphs) had been brought together in the F_1 hybrid (where one dominated the other), but in the second generation they had become sharply separated from one another again and were distributed to different individuals. This separation and redistribution of unit characters in the offspring of hybrid individuals is known as *segregation* and has been found to be a constant feature of all inheritance.

The segregation of characters is by no means a random and irregular process but tends to result in the production of a definite proportion between the numbers of individuals of one type and those of the other, a fact made clear for the first time through Mendel's method of counting the numbers of each. In the experiment in question, for example, he raised 929 plants in the F_2 generation and found that in 705 of them the flower color was red, while in 224 it was white, thus displaying a ratio of approximately three-fourths of the dominants to one-fourth of the recessives (Fig. 17). This ratio, which may be expressed as $\frac{3}{4}:\frac{1}{4}$, 75 per cent:25 per cent, or 3:1, was found to hold true

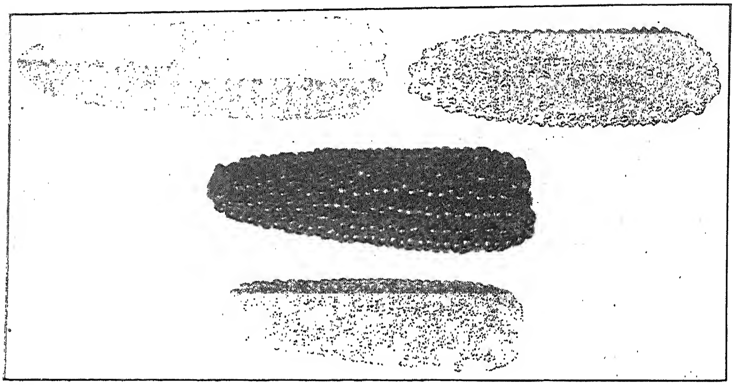


FIG. 20.—Cross between red-kernelled and white-kernelled corn (above). The F_1 (center) is red and in the F_2 ears the segregation of red and white in a ratio of 3:1 can be seen in the kernels.

P = Parent
F = Filial

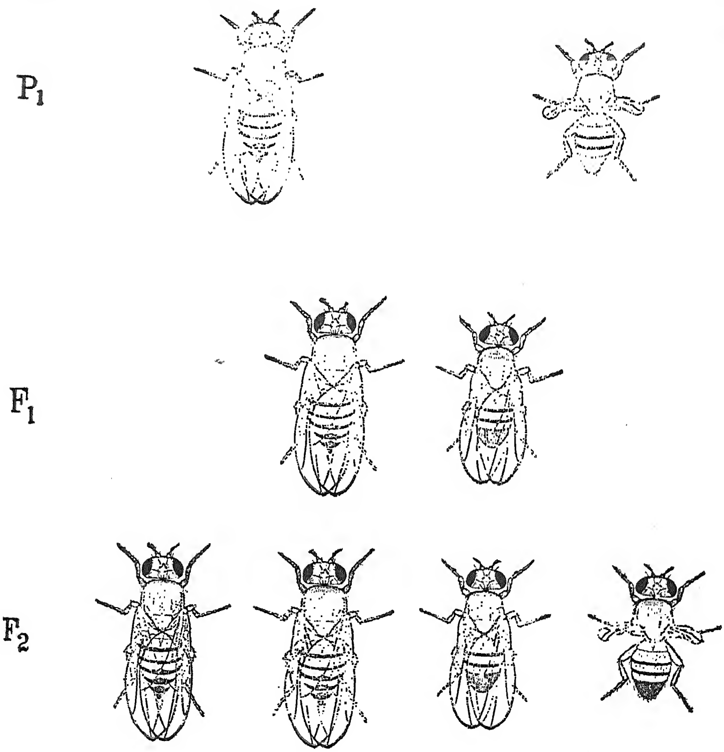


FIG. 21.—Cross between long-winged (wild type) fruit fly and vestigial-winged fly, producing long-winged offspring in the F_1, which if bred to each other give in the next generation (F_2) ¾ long to ¼ vestigial. (*From Morgan.*)

for the F_2 from crosses involving all of the other character-pairs studied, the larger group always being that with the dominant character and the smaller one that with the recessive. The actual counts which Mendel obtained in these various crosses are set forth in Table I. Later work on peas by other investigators has completely confirmed Mendel's results. In the cross involving yellow seeds and green seeds, F_2 generations totaling 179,399 individuals have been recorded (Table II), of which 134,707, or 75.09 per cent, were yellow-seeded and 44,692, or 24.91 per cent, were green-seeded. Other examples of this characteristic mendelian ratio are shown in Figs. 20 and 21.

TABLE II.—SUMMARY OF F_2 RESULTS IN INHERITANCE OF SEED COLOR IN PEAS (*After Johannsen*)

Investigator	Yellow, per cent	Green, per cent	Total
	No. %	No. %	
Mendel, 1865	6,022 (75.05)	2,001 (24.95)	8,023
Correns, 1900	1,394 (75.47)	453 (24.53)	1,847
Tschermak, 1900	3,580 (75.05)	1,190 (24.95)	4,770
Hurst, 1904	1,310 (74.64)	445 (25.36)	1,755
Bateson, 1905	11,902 (75.30)	3,903 (24.70)	15,806
Lock, 1905	1,438 (73.67)	514 (26.33)	1,952
Darbishire, 1909	109,060 (75.09)	36,186 (24.91)	145,246
Totals	134,707 (75.09)	44,692 (24.91)	179,399

It will be shown a little later that this ratio depends on a random union between different gametes, and it should be emphasized that these results of actual breeding do not display simple and exact ratios any more than the tossing of coins or the throwing of dice always give exact and predictable results, and for the same reason. It must not be expected, for example, that with every three red-flowered plants there shall always be associated one with white flowers any more than that in tossing coins heads will invariably alternate with tails. This ratio—and the same is true of the other mendelian ratios—merely indicates what may be expected on the basis of probability. Experience, agreeing with theoretical expectation, has shown that the larger the number of individuals raised, the closer the F_2 ratio approaches $\frac{3}{4}:\frac{1}{4}$, a fact strikingly emphasized in the table just cited (Table II).

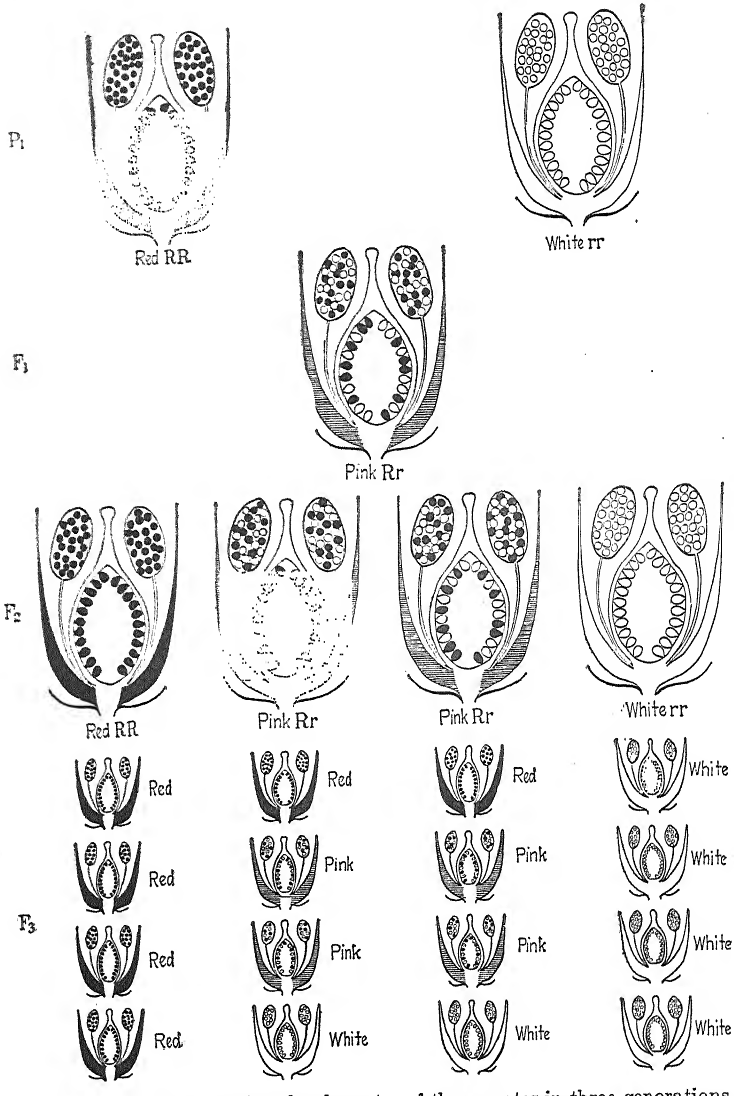


FIG. 22.—Diagram showing the character of the gametes in three generations following a cross between a red-flowered and white-flowered plant. The gametes are represented by pollen grains and ovules, the black ones carrying the factor for red and the white ones that for white. In the (pink) F_1 dominance of red is not complete (corolla shaded) but of the F_1 gametes half carry red and half white, and *none are pink.* In the F_2 one-fourth of the plants are red-flowered and all their gametes carry the factor for red; one-half are *pink-flowered,* with half their gametes carrying red and half white; and one-fourth white-flowered, their gametes all carrying white. The character of the offspring of these F_2 types, when self-fertilized, is shown in the F_3 generation.

Mendel was not content to leave the matter here, however, but studied the progeny of these second-generation hybrids. In the cross involving flower color, he found that the white-flowered F_2 plants bred perfectly true to white flower color through all subsequent generations. The red-flowered plants, however, although looking alike, did not all behave in the same way. About one-third of them bred true to red, but two-thirds produced both red and white offspring in the ratio of about

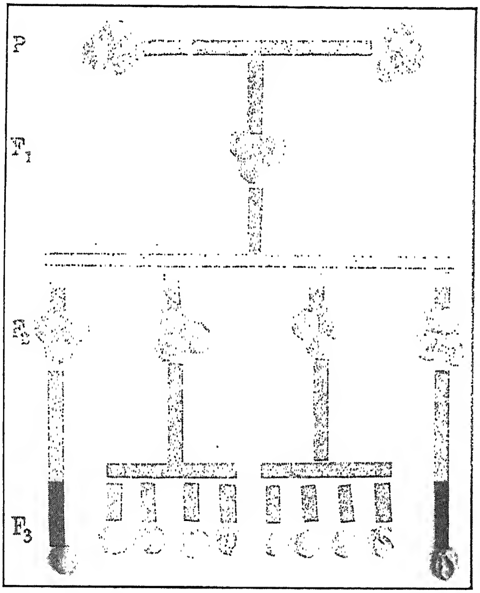


FIG. 23.—Inheritance of seed shape (round and wrinkled) in peas through three generations following a cross of two pure types. (*From White.*)

$\frac{3}{4}:\frac{1}{4}$, thus resembling exactly the F_1 hybrids. The history of three generations following a cross which involves a single character difference is set forth in Figs. 22 and 23.

In the F_2 therefore, approximately one-fourth of the individuals were found to be true-breeding dominant plants, one-half hybrid dominants like the F_1 and one-fourth true-breeding recessives. The fundamental ratio, based on the genetic constitution and breeding behavior of the F_2 individuals, is, therefore, $\frac{1}{4}:\frac{1}{2}:\frac{1}{4}$, and more accurately represents the actual facts than the ratio of $\frac{3}{4}:\frac{1}{4}$, which is based on appearance alone.

The difference between these two ratios, the actual and the visible, is due to the effect of dominance, whereby the pure reds and the hybrid reds resemble each other, thus reducing the three actual classes to only two visibly different ones. In character-pairs which do not exhibit dominance, however, the $\frac{1}{4}:\frac{1}{2}:\frac{1}{4}$ ratio may be observed directly, as in the inheritance of red and white flower color in snapdragons (Fig. 18), and these examples give a clearer insight into the phenomena of segregation than do those where dominance is complete. In the inheritance of coat color in Shorthorn cattle, likewise, it is found that when red is crossed with white the cross-bred (F_1) calves are neither red nor white but a mixture of the two called "roan" (Fig. 19). When two such roan cattle are bred together, they produce on the average about 25 per cent red, 50 per cent roan, and 25 per cent white progeny, a ratio of $\frac{1}{4}:\frac{1}{2}:\frac{1}{4}$. Here there are three visibly different classes, corresponding exactly to the three which are genetically different. It is evident, moreover, that such a trait as roan coat color in Shorthorns is not a true mendelian character at all, in the sense that it is inherited independently and will segregate, but that it is merely the expression of the two contrasted factors when both are present.

In their simplest form, then, the facts as to segregation may be stated as follows: When individuals differing in a single trait are crossed, each trait behaves as a unit, passes intact through individuals of the first generation, where it may or may not be visibly expressed, and emerges unchanged in the second generation. Here one-fourth of the individuals tend to resemble in appearance and breeding behavior, one of the original pure types; one-fourth tend to resemble the other, and one-half to resemble the first generation hybrids.

Explanation of Segregation.—The explanation which Mendel proposed for the occurrence of segregation and its characteristic ratios involved a radically new conception of the manner in which heritable traits are transmitted from generation to generation. As previously stated, the only physical link between parent and offspring is the sexual cell or gamete, which contains factors for every heritable trait which the offspring displays. In the illustration previously employed, then, it may be assumed that all the gametes of the parent red-flowered pea plant carry a factor for redness (in addition of course, to many others), since such a plant, when self-fertilized, produces only red-flowered

offspring. In the same way, all the gametes of the white-flowered plant carry a factor for whiteness. When a cross is made between a red-flowered and a white-flowered plant, two gametes, one carrying red and the other white, unite to produce a plant which is hybrid for this particular character. This hybrid plant obviously must contain in every one of its cells factors for both redness and whiteness. It so happens that in this case only redness becomes visibly expressed in the plant, in contrast to those instances where dominance is absent and where both the contrasting factors influence the appearance of the hybrid individual. Now the essential feature of Mendel's explanation of segregation lies in his assumption as to the manner in which this hybrid red-and-white-carrying individual produces gametes. The fact that where two such hybrids are crossed (or where one is self-fertilized) some of the offspring are true-breeding reds which never produce white-flowered plants among their offspring naturally implies that each of the gametes which united to produce such true-breeding progeny carried a factor for red but none for white. Similarly, the occurrence of pure-breeding white-flowered plants implies the union of two white-carrying gametes which lack factors for red. From these considerations, Mendel drew the inference that when such a hybrid individual, containing factors for both red and white, itself produces gametes, these gametes are not all alike but are of *two different kinds, half of them carrying only the factor for redness and half of them carrying only the factor for whiteness.*

This inference has two implications: first, that every gamete is *pure*, containing only one member of a given factor-pair and thus never showing the hybrid character of the individual producing it; and second, that in the formation of gametes there is a reduction in the amount of genetic material carried, each gamete containing only *half* of the factorial equipment which is present in an ordinary body cell. The essential feature of the mechanism of segregation, therefore, lies in the circumstance that a factor carried by the gametes of one parent and its contrasting factor carried by the gametes of the other parent, come together and coexist for a generation in the cells of the resulting hybrid offspring *without blending or losing their identity;* and that when such a hybrid individual produces its own sexual cells, in turn, these two factors become completely and cleanly separated again, or *segregated* from one another, each of the new gametes

being entirely pure, containing either the one factor or the other but *never both*.

The characteristic $\frac{1}{4}:\frac{1}{2}:\frac{1}{4}$ ratio displayed by the offspring of the hybrid individuals is readily explained if one makes, as did Mendel, one further inference, namely, that in fertilization there is no affinity between gametes carrying the same factors but that the different types *unite at random*, any pollen grain (or sperm) fertilizing any ovule (or egg), and all possible combinations of factors being thereby produced through the operation of chance alone. Since a hybrid produces two kinds of male gametes and two kinds of female ones, as regards any given factor-pair, there will evidently be four possible combinations in fertilization: one involving two factors for one of the members of the pair, another involving two factors for the other member, and two in which unlike factors are united.

The Genotype and Its Representation.—The mechanism of segregation and the appearance of the characteristic ratios which accompany it are perhaps best understood if the common mendelian "shorthand" method of notation is employed and the factorial make-up of individuals and of their gametes is represented by simple letters or formulas. It should be emphasized that every individual is in a genetic sense a *double* structure, since it arises from the union of two gametes and thus draws half of its inheritance from one parent and half from the other. If in the cross which has been used as an example C represents the factor for colored (red) flowers and c[1] the factor for white, the pure-breeding colored-flowered parent, which received the factor C from both of its parents, may, therefore, be represented by the formula CC; and the pure-breeding white-flowered parent by cc (Fig. 24). This formula applies to every *body cell* of the plant. Of course, it should be borne in mind that here only one of the large number of factor-pairs which are actually present is being represented. Now in the cell divisions which just precede the formation of the gametes, cytological research has strikingly confirmed Mendel's assumption that there is a reduction by half in the amount of hereditary material[2] and it is

[1] The dominant (or more dominant) factor of a pair may be designated by a large letter and the other factor by the corresponding small letter, thus indicating immediately which factors comprise a pair (or are allelomorphs).

[2] The chromosomes of the nucleus are in all probability the actual bodies in which the genetic factors are carried, and it has been shown that in the reduction division just preceding the production of gametes the number of chromosomes in the nucleus is halved (p. 139).

therefore justifiable to assume that every sexual cell produced is no longer a double structure (like the body cells) but carries just *half* of each of the factor-pairs which occur in the parent plant. The gametes of the colored-flowered parent in the illustration would, therefore, be represented by *C* and those of the white-flowered parent by *c*. When these two plants are crossed

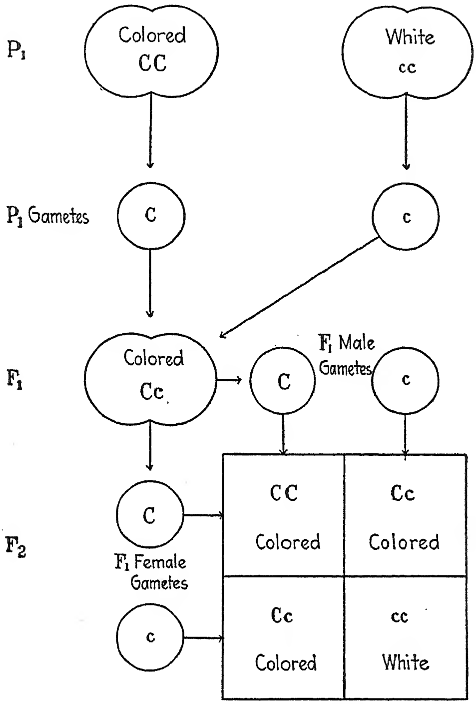


FIG. 24.—Chart showing the behavior of the factors in the cross illustrated in Fig. 17 (colored and white flowers in peas) and giving the genotypes and phenotypes of parents and F_1, the gametes which they produce, and the random union of F_1 gametes to form the three genotypic and two phenotypic classes of F_2 zygotes shown in the checkerboard.

and an egg, *C*, is fertilized by a male gamete, *c* (or *vice versa*), the genetic formula of the resulting hybrid plant is obviously *Cc*. Since color is completely dominant here, this plant appears colored-flowered, but in its factorial make-up (technically known as its *genotype*, as distinguished from its appearance or *phenotype*) there is present a recessive factor for white. If there were no dominance and the hybrids were intermediate in appearance—

pink perhaps—it would, of course, still be represented by the same genotype. When the two members of a given factor pair are alike (as in the parent plants between which this cross was made), the individual is said to be *homozygous* for the factor in question; when the two members are different (as in this hybrid),

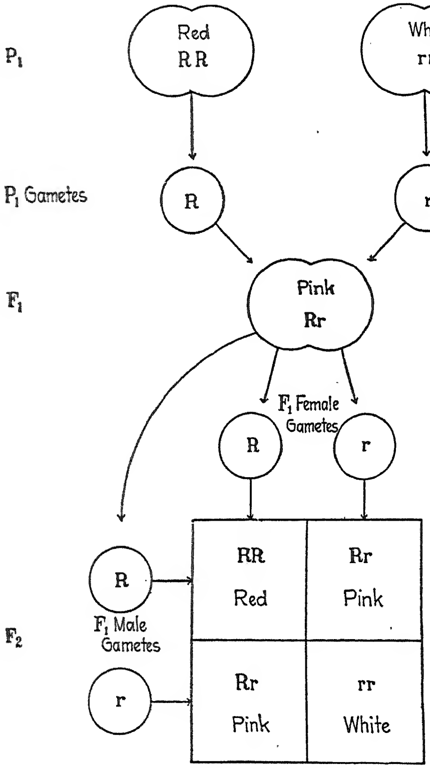


FIG. 25.—Chart showing the behavior of the factors in the cross illustrated in Fig. 18 (red and white flowers in snapdragons) giving the genotypes and phenotypes of parents and (pink) F_1, the gametes which they produce, and the random union of F_1 gametes to form the three genotypic and three phenotypic classes of F_2 zygotes shown in the checkerboard.

it is said to be *heterozygous*. The essence of the phenomenon of segregation lies in the fact that when this heterozygous individual produces gametes, *these* are not hybrid or heterozygous at all, but half of them are *C* and half *c*. Thus the hybrid character of a plant cannot be carried by its gametes, which must be entirely one thing or entirely the other, and are thus *pure*. The

factors C and c, brought in from the original red and white parents, have coexisted in the hybrid without influencing each other in the least and have now parted company, or become segregated.

In the offspring of these hybrid F_1 plants (derived either through cross- or self-fertilization) appear the characteristic $\frac{3}{4}:\frac{1}{4}$ or $\frac{1}{4}:\frac{1}{2}:\frac{1}{4}$ ratios described, and their occurrence is readily explained if it is assumed that fertilization is a purely random process. The gametes of each hybrid parent, after the reduction and segregation which accompany their origin, are of two sorts, approximately half of them carrying the factor C and the other half the factor c, so that if pollen of a hybrid is placed on the stigma of a hybrid and the fertilization which follows is a free and random union, there are four possible combinations which may result in the offspring produced. C male gametes may fertilize C eggs, forming CC plants; C male gametes may fertilize c eggs, forming Cc plants, c male gametes may fertilize C eggs, also forming Cc plants, or c male gametes may fertilize c eggs, forming cc plants. Each of these combinations, on the basis of pure chance, is just as apt to occur as any other, and each should thus give rise to approximately one-fourth of the progeny. The genotypes of the original parents and of the F_1 and F_2 generations for flower color in peas, which shows dominance, and for flower color in snapdragons, which does not, are set forth graphically in Figs. 24 and 25.

Segregation and the Theory of Probability.—The surest evidence that chance alone is concerned in determining the combinations between different types of gametes is the similarity between the results obtained in the F_2 ratios and those which should theoretically appear on the basis of probability as illustrated by such a familiar example as coin-tossing. For instance, if two coins are repeatedly tossed at the same time, the result to be expected from the laws of chance (and the one which the actual results will come closer and closer to reaching as the number of trials increases) is that the combination head-and-head will fall in about one-fourth of the cases, the combination head-and-tail in about one-half of them, and the combination tail-and-tail in the remaining fourth (Fig. 26). This is the ratio which actually occurs in an ordinary F_2 generation, for approximately one-fourth of it is found to be CC plants, which not only have colored flowers but will breed as truly for this character as did their

colored-flowered grandparent; approximately one-half are *Cc* plants, which also have colored flowers but are heterozygous for this character and when selfed or crossed among themselves will behave just as did their immediate parents (the F_1 hybrid) and yield offspring of which about three-fourths are colored-flowered and one-fourth white; and the other fourth are *cc* plants, white-flowered and breeding as truly for this character as did their white-flowered grandparent.

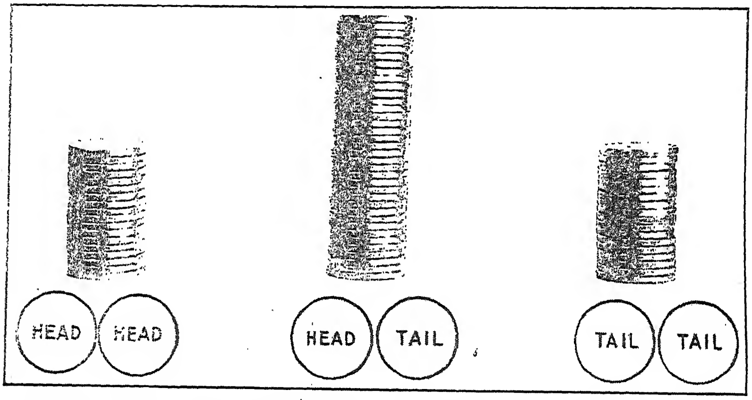


FIG. 26.—The results expected from tossing two coins simultaneously. In one-fourth of the trials, both should fall heads, in one-fourth, both tails, and in one-half there should be one head and one tail. This illustrates the principle of the F_2 mendelian ratio of 1:2:1 resulting from random union of gametes.

The mendelian explanation of the method of inheritance can be put to many tests. What, for instance, should be the result if an F_1 hybrid plant were crossed with the recessive white-flowered type? On Mendel's assumption it would be expected that *half* of the gametes of the hybrid would carry red and half white, while *all* the gametes of the white-flowered plant would carry only the factor for white. If pollen from the white-flowered parent is placed on the stigma of the hybrid, two possible types of fertilization may follow; the union of "white" pollen with "colored" ovules to form heterozygous colored-flowered plants, and of "white" pollen with "white" ovules to form white-flowered plants. These two, on the basis of chance, should occur with equal frequency. Thousands of tests have shown that this result indeed takes place and that a mating between a heterozygous dominant and a recessive may be expected to give offspring half

of which show the dominant character and half the recessive. A similar result holds where dominance is lacking, for among Shorthorn cattle, to which reference has previously been made, it is the rule that a roan animal mated with a white one gives offspring of which about half are roan and half are white.

Tests of this sort unite in confirming the explanation which Mendel gave for the behavior of unit factors in crosses, and the principle of segregation is one of the two major contributions made by him to genetic theory. The conception which it gives of the manner in which heritable traits are transmitted from generation to generation has also led in recent years to some remarkable discoveries as to the actual mechanism of inheritance itself, the details of which will be discussed in a later chapter.

QUESTIONS FOR THOUGHT AND DISCUSSION

32. What is the chief practical importance of discovering laws of inheritance?

33. Give other examples, similar to those mentioned in the text, of a constant association between two series of phenomena which indicates a "cause and effect" relationship between them.

34. Give an example of a group of natural phenomena, the laws governing the behavior of which have not yet been discovered.

35. Give an example of another biological principle which has been found to apply equally well to animals and plants.

36. What advantage has the method of experiment over that of observation alone as a means of studying natural phenomena?

37. Why have the biological sciences been slower to adopt the experimental method of investigation than have the physical sciences?

38. What advantage and what disadvantage have plants over animals as material for the study of heredity?

39. The pedigrees of many domestic animals have long been kept by breeders. Explain.

40. Explain how it can be that individuals which look very much alike breed very differently.

41. Of what practical value is a recognition of the fact that certain traits show dominance?

42. Hybrid animals and plants notoriously fail to breed true. Explain.

43. Why is the F_1 between two homozygous parents as uniform as the parents themselves?

44. In human families traits are often observed to "skip" a generation or two. How do you explain this?

45. Which do you think would be easier to handle in breeding, a trait which shows complete dominance or one which does not? Why?

46. What evidence is there that genetic factors occur in the body cells as well as in the gametes?

47. If red and white beans, in equal numbers, are thoroughly mixed in a bag and two beans at a time drawn out at random, what proportion of the drawings may be expected to give two reds; what proportion one red and one white; and what proportion two whites?

PROBLEMS

Note.—In summer squashes white fruit color is dominant over yellow.

1. If a squash plant homozygous for white is crossed with one homozygous for yellow, what will be the appearance of the F_1? of the F_2? of the offspring of a cross of the F_1 back on its white parent? of the offspring of a cross of the F_1 back on its yellow parent?

2. Let the factor for white fruit be represented by W and that for yellow by w. What kind of gametes as to fruit color will be produced by plants of the genotypes WW, Ww, and ww?

3. What gametes will be produced by the plants involved in the following crosses, in which the genotypes of the parents are given, and what will be the fruit color of the offspring from each cross: $Ww \times ww$; $WW \times Ww$; $ww \times WW$; $Ww \times Ww$?

4. A white-fruited squash plant when crossed with a yellow-fruited one produces offspring about half of which are white and half yellow. What are the genotypes of the parents?

5. If the white-fruited parent in the preceding question is self-fertilized, what will be the fruit color of its offspring?

6. If this same white-fruited parent is crossed with one of its white-fruited offspring mentioned in Question 4, what chance is there of obtaining from this cross a yellow-fruited plant?

7. Two white-fruited squash plants when crossed produce about three-fourths white and one-fourth yellow offspring. What are the genotypes of these two parents? What will each produce if crossed with a yellow-fruited plant?

8. A cross between a white-fruited and a yellow-fruited squash plant produces all white plants. If two of these F_1 white plants are crossed together, what will be the appearance of *their* offspring?

Note.—In guinea pigs, rough or rosetted coat (R) is dominant over smooth (r).

9. If a homozygous rough-coated animal is crossed with a smooth one, what will be the appearance of the F_1? of the F_2? of the offspring of a cross of the F_1 back on its rough parent? on its smooth parent?

10. A certain rough-coated guinea pig bred to a smooth one gives eight rough and seven smooth offspring. What are the genotypes of parents and offspring?

11. If one of the rough F_1 animals in the preceding question is mated to its rough parent, what offspring may be expected?

12. Two rough-coated guinea pigs when bred together produce eighteen rough and four smooth offspring. What proportion of these rough offspring may be expected to be homozygous for this character?

Note.—The polled or hornless condition in cattle (P) is dominant over the horned (p).

13. A certain polled bull is bred to three cows. With cow A, which is horned, a horned calf is produced; with cow B, also horned, a polled calf is produced; and with cow C, which is polled, a horned calf is produced. What are the genotypes of all these four animals and what offspring would you expect from these three matings?

Note.—In man, brown eyes (B) are dominant over blue (b).

14. A brown-eyed man marries a blue-eyed woman and they have eight children, all brown-eyed. What are the genotypes of all the individuals in the family?

15. A blue-eyed man both of whose parents were brown-eyed marries a brown-eyed woman whose father was brown-eyed and whose mother was blue-eyed. They have one child, who is blue-eyed. What are the genotypes of all the individuals mentioned?

Note.—Assume that in man, right-handedness (R) is dominant over left-handedness (r).

16. A right-handed man whose mother was left-handed marries a right-handed woman who has three brothers and sisters, two of whom are left-handed. What chance will the children of this marriage have of being left-handed?

Note.—In Four-o'clock flowers, red flower color (R) is incompletely dominant over white (r), the heterozygous plants being pink-flowered.

17. In the following crosses, in which the genotypes of the parents are given, what are the gametes produced by each parent and what will be the flower color of the offspring from each cross:

$$Rr \times RR;\ rr \times Rr;\ RR \times rr;\ Rr \times Rr?$$

18. If a red-flowered Four-o'clock plant is crossed with a white-flowered one what will be the flower color of the F_1? of the F_2? of the offspring of a cross of the F_1 back on its red parent? on its white parent?

19. If you wanted to produce Four-o'clock seed *all* of which would yield pink-flowered plants when sown, how would you do it?

Note.—In Andalusian fowls the heterozygous condition of the factors for black plumage (B) and white (b) is blue; and in Shorthorn cattle the heterozygous condition of red coat color (R) and white (r) is roan.

20. It has long been known that blue Andalusian fowls do not breed true to the blue color of their plumage. How do you explain this?

21. What offspring will a blue Andalusian fowl have if bred to birds of the following plumage colors: (1) black; (2) blue; (3) white?

22. If two roan Shorthorn cattle are mated, what chance will their offspring have of resembling their parents in coat color?

23. In what respect are characters which behave like plumage color in Andalusian fowls and flower color in four-o'clocks easier to deal with in breeding work than one which behaves like fruit color in squashes or coat type in guinea pigs?

Note.—In poultry, rose comb is dominant over single comb.

24. A farmer believes that some of his rose-combed Wyandotte fowls may carry a factor for single comb. Can you suggest a method for finding out which fowls are heterozygous?

25. Two black female mice are crossed with a brown male. In several litters female 1 produced nine blacks and seven browns; female 2 produced seventeen blacks. What deductions can you make concerning inheritance of black and brown coat color in mice? What are the genotypes of the parents in this case?

26. If one of the sons of female 2 of the previous question is back-crossed to the mother, what would the resulting offspring look like?

27. A purple-flowered Jimson weed when self-fertilized gives thirty purple-flowered and nine white-flowered offspring. What can you conclude from this as to the inheritance of flower color in this species? What proportion of the purple-flowered offspring may be expected to breed true to purple?

28. In adzuki beans, a plant with light-mottled seeds, when selfed, produces offspring about one-fourth of which are dark-mottled, one-half light-mottled, and one-fourth unmottled. What offspring would you expect from a cross of a dark-mottled plant with an unmottled one?

29. Assume that in a particular species of plants colored flowers are dominant over white ones, and that (as in beans) the flowers are *self-fertilized* in nature. Assume that one heterozygous colored-flowered

plant, *Cc*, becomes established on an island where no other individuals of this species exist, and that its offspring thrive and multiply there *in great numbers*. Assume also that it is an annual plant and that thus there is no chance for members of one generation to cross with those of another. What will the *fifth* generation of descendants look like as to flower color?

30. Make just the same assumptions as in Question 29, *except* that the plant in question (like sunflowers and many other plants and like all animals) is *self-sterile* and must be crossed with another plant to set fertile seed; that two heterozygous plants, *Cc* and *Cc*, are the original invaders; and that the individuals of each generation breed freely together. What will the fifth generation of *these* plants look like as to flower color?

REFERENCE ASSIGNMENTS

19. Give an example from some other science of the framing of an hypothesis and its subsequent verification.

20. Describe the process of discovery of a scientific law by one of the following

1. Newton
2. Pasteur
3. Galileo.

21. Give an account of Mendel's life.

22. Give another example of a man not a professional scientist whe made an important contribution to scientific theory.

Note.—As preliminary to the following three questions, read Mendel's original paper (see Bibliography).

23. What reasons did Mendel give for his choice of peas as experimental plants?

24. To what other experimenters did Mendel refer in his paper and what contributions did their results make to his theory?

25. What character did Mendel find in peas which did not show complete dominance?

26. In what respect did Naudin anticipate the conclusions reached by Mendel? Why did he fail to discover the general laws of inheritance formulated by Mendel?

27. How does the idea that the genetic factors are located in the chromosomes help to explain the fact that factors co-exist in a hybrid individual for a generation without blending or losing their identity?

28. Give an instance in which practical breeders have been guided by principles similar to those formulated by Mendel without recognizing them as general laws of inheritance.

29. Give the derivation of the following terms and explain in what way each is appropriate:

Gene	Homozygous	Genotype
Allelomorph	Heterozygous	Phenotype

CHAPTER IV

MENDEL'S LAWS OF INHERITANCE. II

It has been seen that Mendel's genius in studying the inheritance of single characters by themselves led him to a discovery of the principle of segregation, the essential features of which have been discussed in the preceding chapter. This principle is concerned with the hereditary transmission of but one of the many factor-pairs which constitute the individual. In most breeding problems, however, it is necessary to be able to follow not only a single character but a whole series of them at once, and to understand how they behave with relation to each other in their passage from generation to generation.

The Principle of Independent Assortment.—Mendel studied seven pairs of characters in peas, involving seed color, seed surface, flower color, vine height, color of unripe pods, pod shape, and position of flowers. A study of the results of experiments in which plants differing in two or more of these characters were crossed led to his discovery of the second major principle of mendelian inheritance, that "the relation of each pair of different characters in hybrid union is independent of the other differences in the two original parental stocks."

Mendel was led to a recognition of this principle by the results of a cross made between a pea plant having round and yellow seeds and one having wrinkled and green ones.[1] In this case he found, of course, that the F_1 hybrids were all round-seeded and yellow-seeded, since these two characters are both completely dominant. When two of these F_1 hybrids were crossed, however (or when one of them was self-fertilized), and an F_2 generation raised therefrom, he found that in this generation there appeared not only the two original combinations of characters—round with yellow and wrinkled with green—but two *new* combinations, *round with green and wrinkled with yellow*. These four kinds of plants, moreover, were not equal in numbers but appeared in a rather definite ratio, the successful interpretation of which

[1] Such a cross as this, which involves *two* character differences, is technically known as a *dihybrid* cross.

was Mendel's second great contribution to genetic theory. He raised 556 second-generation plants, and the counts which he obtained were as follows:

315 round and yellow.
108 round and green.
101 wrinkled and yellow.
32 wrinkled and green.

Considering either of these character-pairs *alone*, it is found that approximately three-fourths of the plants show the dominant trait and one-fourth show the recessive, as a knowledge of the principle of segregation would lead one to expect. Thus, of the total 556 plants, 423, or 76.08 per cent are round-seeded and 133, or 23.92 per cent, are wrinkled-seeded; and 416, or 74.82 per cent, are yellow-seeeded and 140, or 25.18 per cent, are green-seeded. When both character-pairs are considered *together*, however, it is found that the segregation into three-fourths and one-fourth which occurs in each pair when considered alone is *entirely independent* of the similar segregation which takes place in the other pair. Thus, of the three-fourths of the entire group of plants which are round-seeded, approximately three-fourths, in turn, are yellow-seeded and one-fourth are green; and of the other fraction (one-fourth) which are wrinkled-seeded, three-fourths, again, are yellow-seeded and one-fourth green. This leads to the result that *three-fourths of three-fourths* of the entire number of plants in the F_2 generation, or nine-sixteenths of the entire number of plants, show both dominant characters (round and yellow); *one-fourth of three-fourths*, or three-sixteenths, show one dominant and one recessive (round and green); *three-fourths of one-fourth*, or again three-sixteenths, show the other combination of dominant and recessive (wrinkled and yellow), and only *one-fourth of one-fourth*, or one-sixteenth, show both recessive characters (wrinkled and green). The counts which Mendel actually obtained in his experiment (315:108:101:32) came very close to these proportions, and he therefore inferred that the second generation from a cross involving two character-pairs will show four kinds of individuals, approximately in the ratio of $\frac{9}{16}:\frac{3}{16}:\frac{3}{16}:\frac{1}{16}$, or 9:3:3:1. His results with other characters in peas and similar crosses which have been made many times by others with all sorts of animals and plants leave no doubt that this ratio is the true one for such dihybrid crosses

which show dominance. Similar cases of dihybrid inheritance in *Drosophila* and squashes are shown in Figs. 27 and 28.

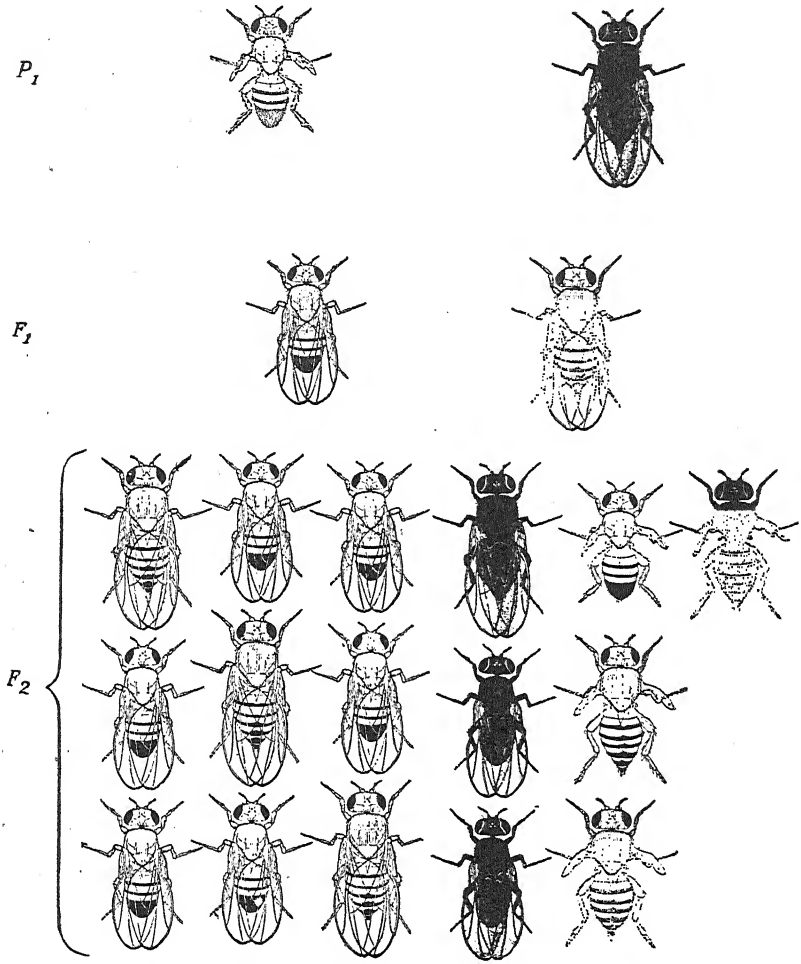


FIG. 27.—The independent inheritance of two pairs of characters in *Drosophila*. A pure long-winged fly with ebony body mated with a vestigial-winged, gray-bodied one produces all long-winged, gray-bodied flies in F_1. These when inbred produce an F_2 generation consisting of $\frac{9}{16}$ long, gray; $\frac{3}{16}$ long, ebony; $\frac{3}{16}$ vestigial, gray and $\frac{1}{16}$ vestigial ebony. (*From Morgan, Sturtevant, Muller and Bridges, courtesy Henry Holt and Co.*)

This *independent assortment* of two character-pairs is made still more manifest by the fact that the particular combination in which the characters are brought into a cross makes no

difference at all in the manner in which they are assorted and recombined in the F_2. In the example cited both dominant

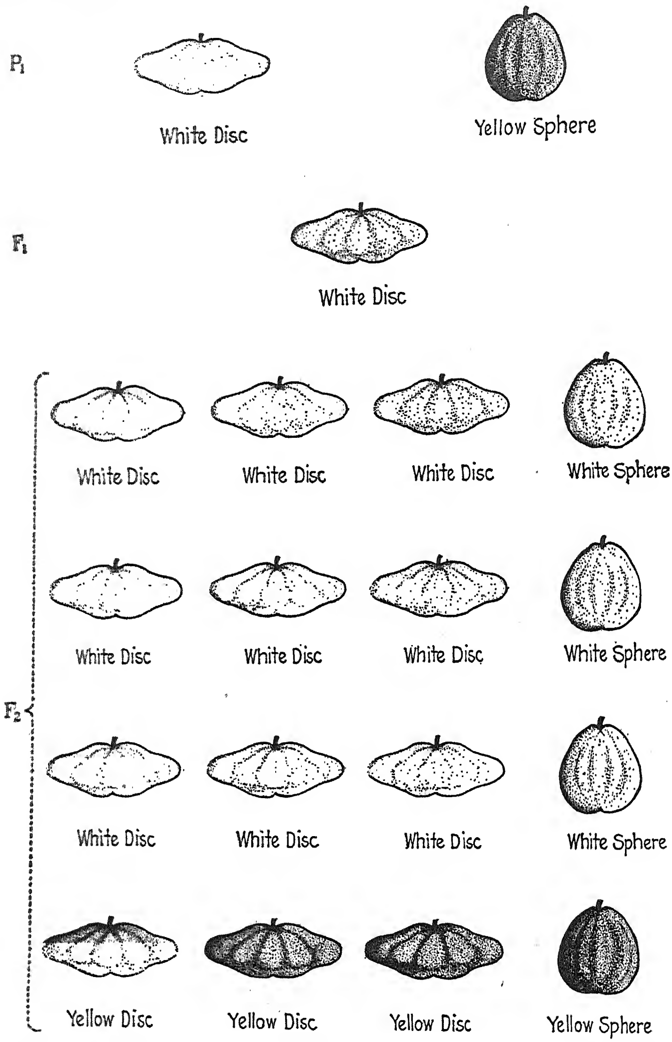


FIG. 28.—The inheritance of two pairs of characters in summer squashes, illustrating Mendel's law of independent assortment. White is dominant over yellow and "disc" shape over "sphere." In F_2 there result $\frac{9}{16}$ white disc, $\frac{3}{16}$ white sphere, $\frac{3}{16}$ yellow disc and $\frac{1}{16}$ yellow sphere plants.

characters were brought in by one parent and both recessives by the other, but exactly the same results are obtained in

the F_2 if instead of crossing round and yellow with wrinkled and green, round and green is crossed with wrinkled and yellow. The F_2 generation consists in this case of nine-sixteenths round yellow, three-sixteenths round green, three-sixteenths wrinkled yellow, and one-sixteenth wrinkled green. The fact of independent assortment again emphasizes the soundness of Mendel's conception of the individual as a series of independent units.

Explanations of Independent Assortment.—Perhaps it would be easier to understand what is involved in the principle of independent assortment if the factors are again represented by letters and the genotypes of the various individuals and the gametes which they form are studied in this way. Let the factor for round seeds be represented by R and that for wrinkled seeds by r; and the factor for yellow seeds by Y and for green seeds by y. Mendel's original round, yellow parent plant would thus be represented by the formula $RR\ YY$ and his wrinkled, green plant by $rr\ yy$. It has already been noted that the gametes carry just *half* of the factorial constitution of the parent individual, so that in this case one parent would produce gametes all of which carried $R\ Y$ and the other, gametes all of which carried $r\ y$; and the resulting F_1 hybrid offspring arising from a union of two of these gametes would consequently have the genotype $Rr\ Yy$. Now the crux of the problem, as in that of segregation, lies in the kinds of gametes produced by this F_1 individual. When the character of seed surface alone is considered (as was flower color in discussing segregation), it is found that the F_1 Rr individual produces gametes half of which carry R and half r. It is quite clear, however, that every gamete must necessarily contain within itself not only a factor for seed surface but one for seed color as well, and, indeed, one for every other character of the plant. Half of these same gametes must, therefore, contain the factor Y and half the factor y; but in any given gamete it seems to be *purely a matter of chance* as to whether the factor for round seeds is associated with that for yellow seeds or whether it is associated with that for green seeds. The particular combination of factors which enters the F_1 plant from each parent (round with yellow and wrinkled with green in this case) has no effect whatever upon the way in which they are associated in the gametes formed by this F_1 plant. *Their assortment is independent.* Of that half of the gametes which carry the factor for round seeds,

a half in turn (or a quarter of the whole) will carry yellow and a half will carry green; and of that half which carry the factor or wrinkled seeds, a half will also carry yellow and a half green. The F_1 hybrid may, therefore, be expected to produce four kinds of gametes in approximately equal numbers: $R\,Y$, $R\,y$, $r\,Y$, and $r\,y$.

Now if two such F_1 plants, each of them producing four kinds of gametes, are crossed, there will obviously be sixteen possible combinations among their gametes, for there will be four kinds of pollen grains and four kinds of egg cells. The union of these gametes in fertilization is here, too, apparently entirely a random one, any type of pollen grain being as likely to effect fertilization as any other; and any type of egg cell being as likely to be fertilized as any other, no selective preference being exhibited between them. The sixteen possible combinations which appear among the F_2 offspring will, therefore, tend to be equally numerous. The parents, F_1 and F_2 of the cross which has been used as an example are represented diagrammatically in Fig. 29[1] both as to their genotypes and their appearance, the sixteen squares in F_2 representing the sixteen possible combinations of gametes. A count of these squares makes clear how the 9:3:3:1 ratio arises, for nine out of these sixteen individuals are in appearance round and yellow, three are round and green, three are wrinkled and yellow, and only one is wrinkled and green.

This principle may perhaps be made a little clearer by a simple comparison. Assume that of all the men in a given country half are brown-eyed and half are blue-eyed; and that half are right-handed and half left-handed. Assume further that there is no connection whatever between these two characters, so that of the brown-eyed men approximately half are right-handed and half left-handed, and of the blue-eyed ones, the same. There will thus be four kinds of male individuals in about equal numbers; the brown-eyed and right-handed, the

[1] The simplest way to determine the expected combinations produced by random union among gametes is to arrange the gametes from the two sexes on two sides of a checkerboard as in Fig. 29. In the row of squares from each gamete are written the factors contributed by that gamete. Each square at the intersection of two rows represents the zygote formed by the union of one male and one female gamete, and the genotype and phenotype of each expected type of offspring (sixteen in this case) may be read directly from the squares.

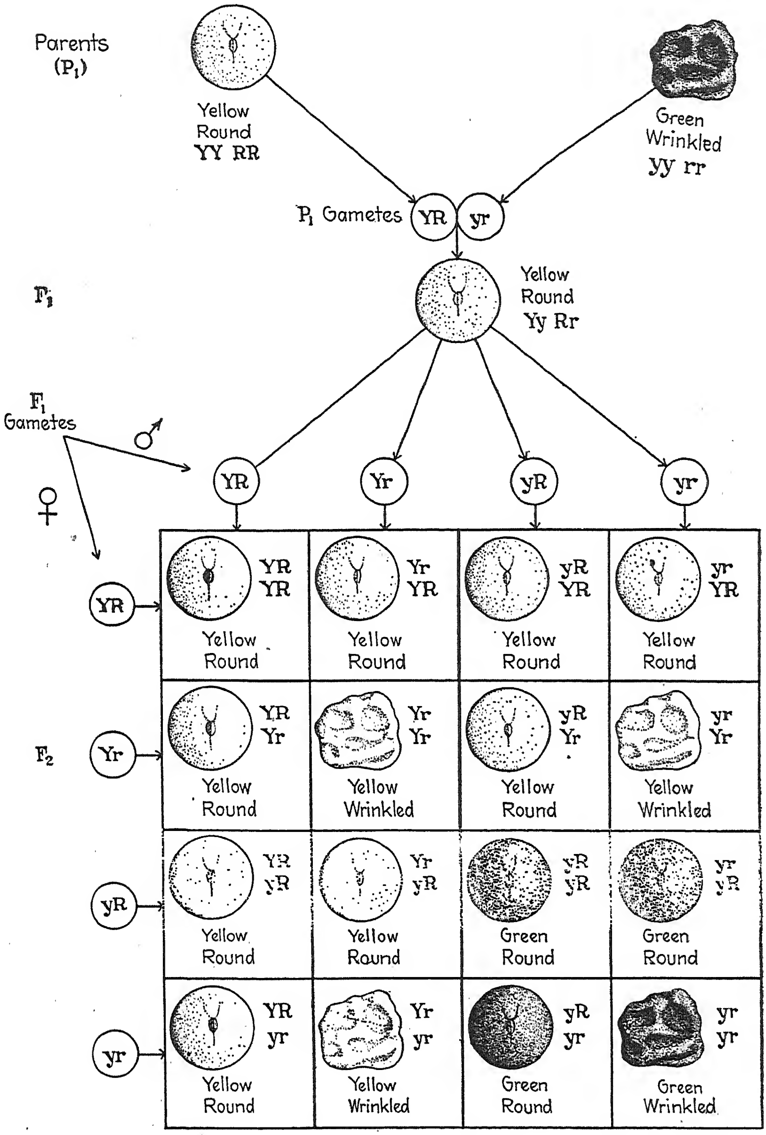


FIG. 29.—Diagram showing the independent assortment in peas of two pairs of characters in which dominance is complete. In a cross between a plant homozygous for yellow and round seeds and a green, wrinkled-seeded one, the appearance, genotype and gametes of parents and F_1 are shown. The results of random union between the four types of gametes formed by the F_1 heterozygote are presented in the F_2 checkerboard.

brown-eyed and left-handed, the blue-eyed and right-handed and the blue-eyed and left-handed. Finally, assume that the women are divided in just the same way; and that in determining what matings shall take place between men and women, eye color and right- and left-handedness play no part whatever, a brown-eyed individual being just as likely to mate with a blue-eyed as with a brown-eyed one, and a right-handed individual with a left-handed as with a right-handed one. The existence of four types of men and of four types of women in about equal numbers will thus result in sixteen kinds of matings, each as likely to take place as any other, a condition precisely parallel to that which occurs in the union of the four types of gametes of an F_1 dihybrid to form the F_2 generation.

Difference between Genotype and Appearance.—It is obvious, however, that in the F_2 generation the sixteen types will not all be *visibly* different, since some of the combinations will look alike, as dominance causes heterozygous individuals to look like homozygous dominant ones. As far as actual appearance goes, therefore, there will be only *four* kinds of individuals instead of sixteen, and some of these groups will be much more numerous than others.

The way in which new combinations of characters are brought about through hybridization is therefore evident, but it should be remembered that the appearance of many of these F_2 individuals does not give an accurate idea of their genetic constitution, for they may be heterozygous in one or both factors and will therefore not breed true. There are, for example, four kinds of round-seeded and yellow-seeded individuals: those with the genotype *RR YY*, which are homozygous for both round and yellow, and will breed true if inbred; those with the genotype *RR Yy*, which are homozygous for round but heterozygous for yellow, and will therefore breed true to round but not to yellow; those with the genotype *Rr YY*, which are heterozygous for round and homozygous for yellow and will breed true to yellow but not to round; and those with the genotype *Rr Yy*, which are heterozygous for both and will breed true to neither character but will produce offspring exactly like those of the F_1. A study of the squares in Fig. 29 shows that these four types are not found in equal numbers but in the proportion of 1:2:2:4, respectively. Mendel tested this assumption experimentally and inbred all of his 315 F_2 plants which bore round and yellow seeds.

3:6:3:2:1

He obtained offspring from 310 of them, of which 38 produced plants all bearing round and yellow seeds; 65 produced plants all bearing round seeds but some yellow and some green; 60

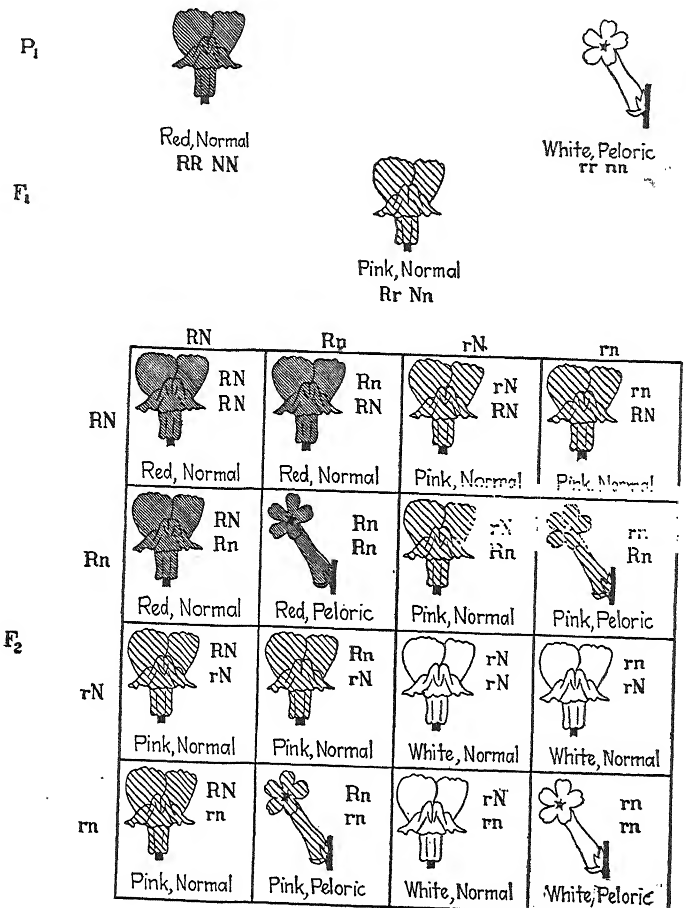


FIG. 30.—Diagram showing the independent inheritance in snapdragons of two pairs of characters, in one of which dominance is complete and in the other of which it is lacking. In a cross between a plant homozygous for red flowers of normal shape and one with white and abnormal (peloric) flowers, the appearance and genotype of parents, F_1 and F_2 are shown.

produced plants all bearing yellow seeds but some round and some wrinkled; and 138 produced plants of all four types.

Of course, it should be borne in mind that the characteristic 9:3:3:1 ratio is to be found only when both characters show

complete dominance. If dominance is partial or absent, the heterozygous individuals are different in appearance from the pure ones, and more than four F_2 groups will thus be visibly distinguishable. The results of a dihybrid cross in which one character-pair shows complete dominance and the other does not are shown in Fig. 30. The presence or absence of dominance, however, has no bearing whatever on the fundamental fact of the independence of assortment of the factors in the gametes.

The Trihybrid.—When individuals differing in *three* characters are crossed (a trihybrid cross), the situation is naturally more

	RYC	RYc	RyC	Ryc	rYC	rYc	ryC	ryc
RYC	RYC RYC	RYc RYC	RyC RYC	Ryc RYC	rYC RYC	rYc RYC	ryC RYC	ryc RYC
RYc	RYC RYc	RYc RYc	RyC RYc	Ryc RYc	rYC RYc	rYc RYc	ryC RYc	ryc RYc
RyC	RYC RyC	RYc RyC	RyC RyC	Ryc RyC	rYC RyC	rYc RyC	ryC RyC	ryc RyC
Ryc	RYC Ryc	RYc Ryc	RyC Ryc	Ryc Ryc	rYC Ryc	rYc Ryc	ryC Ryc	ryc Ryc
rYC	RYC rYC	RYc rYC	RyC rYC	Ryc rYC	rYC rYC	rYc rYC	ryC rYC	ryc rYC
rYc	RYC rYc	RYc rYc	RyC rYc	Ryc rYc	rYC rYc	rYc rYc	ryC rYc	ryc rYc
ryC	RYC ryC	RYc ryC	RyC ryC	Ryc ryC	rYC ryC	rYc ryC	ryC ryC	ryc ryC
ryc	RYC ryc	RYc ryc	RyC ryc	Ryc ryc	rYC ryc	rYc ryc	ryC ryc	ryc ryc

FIG. 31.—Checkerboard showing the 64 possible combinations in F_2 from a cross of a homozygous round-seeded, yellow-seeded, colored-flowered pea plant with a wrinkled-seeded, green-seeded, and white-flowered one.

complex, but the principle of independent assortment still holds good. If a homozygous round-seeded, yellow-seeded, and colored-flowered pea plant is crossed with a wrinkled-seeded,

green-seeded, and white-flowered one, the F_1 hybrids are all, of course, round-seeded, yellow-seeded, and colored-flowered. The F_2, however, will be much more complex than a dihybrid F_2. Since the assortment of these three sets of factors in the gametes is independent, there will evidently be *eight* kinds of gametes, one-half of one-half of one-half, or one-eighth, carrying the factors for round, yellow and colored; one-eighth those for round, yellow, and white; one-eighth those for round, green, and colored; one-eighth those for round, green, and white; one-eighth those for wrinkled, yellow, and colored; one-eighth those for wrinkled, yellow, and white; one-eighth those for wrinkled, green, and colored, and one-eighth those for wrinkled, green, and white.

In the F_2 generation produced by random union among these eight kinds of gametes there will evidently be sixty-four equally possible and theoretically equally frequent combinations. As in the dihybrid F_2, many of these will be similar and many others will appear to be so but will have different genotypes. These sixty-four F_2 types, with their appearance and their genotypic constitution, are presented in a checkerboard (Fig. 31), which represents the results of a trihybrid cross. A study of this group shows that there are only eight *visibly different* forms: $^{27}/_{64}$ (or $^3/_4$ of $^3/_4$ of $^3/_4$) have all three dominant characters; three groups each with $^9/_{64}$ (or $^3/_4$ of $^3/_4$ of $^1/_4$) show two of the dominants and one of the recessives; three groups each with $^3/_{64}$ (or $^3/_4$ of $^1/_4$ of $^1/_4$) show one dominant and two recessives; and only $^1/_{64}$ (or $^1/_4$ of $^1/_4$ of $^1/_4$) show all three recessive characters. The ratio of 27:9:9:9:3:3:3:1 is, therefore, typical for such a trihybrid, where all the characters show complete dominance.

As in the monohybrid and dihybrid crosses, many of these F_2 individuals which look alike are quite different genotypically and all produce very different offspring when inbred (Table III). Of the twenty-seven sixty-fourths which appear round, yellow, and colored, for example, there are eight kinds of plants, each of which will breed differently from the rest. Of course, where one or more of the characters studied show incomplete dominance, so that heterozygous individuals may be distinguished at sight from homozygous ones, the number of visibly different classes will be larger than eight, and the ratio between them will be correspondingly altered.

TABLE III.—THE THEORETICAL NUMBER OF INDIVIDUALS, WITH THEIR GENOTYPES AND BREEDING BEHAVIOR, EXPECTED IN F_2 FROM A TRIHYBRID CROSS OF A ROUND, YELLOW-SEEDED, COLORED-FLOWERED VARIETY OF PEAS WITH A WRINKLED, GREEN-SEEDED, WHITE-FLOWERED ONE (*After Jones*)

Number of individuals	Genotype class	Phenotype class	Ratio of phenotypes	Breeding behavior
1	*RR YY CC*	Round Yellow Colored	27	Breeds true.
2	*Rr YY CC*			Segregates round-wrinkled, 3:1.
2	*RR Yy CC*			Segregates yellow-green, 3:1.
2	*RR YY Cc*			Segregates colored-white, 3:1.
4	*Rr Yy CC*			Segregates round-wrinkled, yellow-green 9:3:3:1.
4	*Rr YY Cc*			Segregates round-wrinkled, colored-white, 9:3:3:1.
4	*RR Yy Cc*			Segregates yellow-green, colored-white, 9:3:3:1.
8	*Rr Yy Cc*			Segregates round-wrinkled, yellow-green, colored-white, 27:9:9:9:3:3:3:1.
1	*RR YY cc*	Round Yellow White	9	Breeds true.
2	*RR Yy cc*			Segregates yellow-green, 3:1.
2	*Rr YY cc*			Segregates round-wrinkled, 3:1.
4	*Rr Yy cc*			Segregates round-wrinkled, yellow-green, 9:3:3:1.
1	*RR yy CC*	Round Green Colored	9	Breeds true.
2	*RR yy Cc*			Segregates colored-white, 3:1.
2	*Rr yy CC*			Segregates round-wrinkled, 3:1.
4	*Rr yy Cc*			Segregates round-wrinkled, colored-white, 9:3:3:1.
1	*rr YY CC*	Wrinkled Yellow Colored	9	Breeds true.
2	*rr Yy CC*			Segregates yellow-green, 3:1.
2	*rr YY Cc*			Segregates colored-white, 3:1.
4	*rr Yy Cc*			Segregates yellow-green, colored-white 9:3:3:1.
1	*rr yy CC*	Wrinkled Green Colored	3	Breeds true.
2	*rr yy Cc*			Segregates colored-white, 3:1.
1	*rr YY cc*	Wrinkled Yellow White	3	Breeds true.
2	*rr Yy cc*			Segregates yellow-green, 3:1.
1	*RR yy cc*	Round Green White	3	Breeds true.
2	*Rr yy cc*			Segregates round-wrinkled, 3:1.
1	*rr yy cc*	Wrinkled Green White	1	Breeds true.
64				

In the same way, individuals differing in four characters may be brought together in a cross, and in such a case the F_2 is even more complicated than that of a trihybrid, sixteen kinds of gametes being produced by the F_1 and 256 possible combinations resulting in the F_2. Crosses of this complexity are rarely worked out in detail and the ratios determined, on account of the very large number of F_2 individuals which must be raised. In actual practice, however, individuals differing in more than four characters are often crossed and although a large and representative

F_2 may not be grown, it is often useful to be able to understand how frequently a particular combination of traits might be expected to appear in such an F_2 and thus to be able to estimate the probability of its occurrence in a given number of F_2 individuals which might be raised.

A study of these complex crosses brings out several points which should be kept in mind. First, as the number of characters involved in a given cross increases, the number of possible character combinations in the F_2 increases greatly, every added character-pair multiplying the number of possible combinations by four, the number of genotypically different combinations by three, and of visibly different combinations (when dominance is complete) by two, as indicated by the accompanying table (Table IV). Second, as the number of characters involved increases, the chance of recovering one of the original parent types in the F_2 grows rapidly less. When a single factor-pair is involved, one in 4 of the F_2 will resemble one of the original parents in appearance and genotype; when two factors are involved, one in 16; when three, one in 64, when four, one in 256, and so on.

TABLE IV.—THE RELATION BETWEEN THE NUMBER OF FACTOR-PAIRS INVOLVED IN A CROSS AND THE NUMBER OF PHENOTYPIC AND GENOTYPIC CLASSES IN F_2

Number of factor-pairs involved in the cross	Number of visibly different F_2 classes of individuals if dominance is complete	Number of different kinds of gametes formed by the F_1 hybrid	Number of genotypically different combinations	Number of possible combinations of F_1 gametes
1	2	2	3	4
2	4	4	9	16
3	8	8	27	64
4	16	16	81	256
n	2^n	2^n	3^n	4^n

A study of the assortment and recombination of factors which goes on in the F_2 when more than one factor-pair is involved makes it clear how readily new character combinations are formed and emphasizes the importance of hybridization as a cause of increased variation, a fact which has already been noted in the discussion of variation. A thorough understanding of the principles which are concerned in this process renders it easy to control and to predict the appearance of new types of

animals and plants, and is one of the chief contributions which the science of genetics has made to the art of practical breeding.

Later Modifications of Mendel's Laws.—The dramatic rediscovery of Mendel's work in 1900 and the recognition of its very great importance to a knowledge of heredity led immediately to an eager study of other animals and plants by many investigators in an endeavor to determine how wide was the application of Mendel's laws and whether or not they would need modification. The number of students of genetics has since increased steadily from year to year, and this field of investigation is now one of the most active in all biology. Hundreds of species have been studied and thousands of breeding experiments performed. As a result there is now a very great mass of facts with regard to the manner of inheritance of all sorts of traits in plants and animals and in man himself, and we are now in a far better position to formulate laws of inheritance than was Mendel. Perhaps the most striking result of all this activity, however, is that Mendel's main conclusions still remain, essentially unchanged, as the cornerstone of the science of genetics.

These results of later research however, have added many details to our knowledge of heredity and have resulted in the discovery of several entirely new principles. These various amplifications will be discussed in later chapters, but it may be well to mention them briefly here in concluding the preliminary statement of mendelism as a whole.

Variability of Factor Expression.—It has been noted that Mendel did not distinguish clearly between the visible *character* and the fundamental *factor* which produced it. Very many cases have been observed, however, in which individuals of exactly the same factorial constitution may differ greatly in their appearance if they have been developed under different environments. Examples of such variations due solely to the environment were presented in a previous chapter. The principles of Mendel, therefore, are applied today to the factors which form the genetic constitution of the individual rather than to the characters or traits which are their visible expressions.

All the characters which Mendel studied showed complete dominance, but very many instances have since been found in which dominance is only partial or is absent, factors in a heterozygous condition expressing themselves very differently from homozygous recessives or dominants.

Still more important are the many instances now known in which various factor-pairs interact upon one another in such a way that the characters produced are markedly affected. The classic example of this is perhaps the comb of poultry. If the factor for "rose" comb and that for "pea" comb are united in a cross, the resulting offspring have combs which are neither rose nor pea but an entirely different type, "walnut." In the same way, the kernel color of corn may be affected by a whole series of factors, each of which has some influence upon the others. Whether these mutual effects are due to fairly simple chemical phenomena or are more complex in their causes is not known, but geneticists today are inclined to look upon each factor as influencing, more or less radically, the effect of all the other factors. They are also abandoning the earlier idea that a single factor determines but a single character of the individual, for in many instances a factor which is known from breeding tests to be a single unit is found to affect all sorts of characters in all parts of the individual.

The Inheritance of "Size" Characters.—Characters which differ from one another in degree rather than in kind and must, therefore, be studied by measurements of one sort or another are called "size" or *quantitative* characters. Such are differences in length, weight, speed, yield, and other traits. Mendel studied one such character—length of vine in peas—and found that it behaved like all the rest, tallness being completely dominant over dwarfness, and all the F_2 plants being clearly separable into these two types. In many similar size characters which have since been studied, however, the situation has been found to be more complex than this. The F_1 in such instances is usually intermediate in size between the two parents, and segregation, while apparent, is not striking in the F_2, the individuals ranging all the way from one grandparental extreme to the other. Such cases were long thought to be exceptions to Mendel's laws, but they are now rather satisfactorily explained by assuming the existence of a considerable number of factors, each of them affecting the same size character and each segregating independently of the rest. The inheritance of quantitative characters will be discussed in much more detail later, for it has extended the conception of mendelism to a group of traits where its operation was long questioned. It so happens, too that these characters are, in general, of much greater eco-

nomic importance than qualitative ones, and it is thus particularly noteworthy that their inheritance can, in a measure, be understood and controlled.

The Linkage of Factors.—Perhaps the most important modification of mendelism and one which should rank with segregation and independent assortment as a third major law of inheritance is the principle of *linkage* between factors. As previously mentioned, Mendel noted the independence which each factor-pair displayed in its inheritance. As long as only a few characters in a given species were studied, this principle was found to be universally valid, but fairly early in the course of mendelian investigations cases began to be reported where two or more characters, introduced into a cross together, tended to stay together or to remain "linked" in their passage from generation to generation, rather than to show that independence of assortment assumed by Mendel. They were long regarded as exceptional instances, and various hypotheses were put forward to account for their occurrence. It was not until the researches of Morgan and his students on the fruit fly (*Drosophila*) began that a logical explanation for the whole matter was obtained. Morgan noted that in this species there are four groups of factor-pairs within each of which the factors tended to stay together or remain "linked" in inheritance. Characters belonging to different groups showed typical mendelian independence of assortment. It was then observed that in the nuclei of the cells of *Drosophila* there are four pairs of rod-like, deeply staining structures called *chromosomes*, and the idea was developed that these chromosomes are the actual physical seat of the genetic factors. The number of these bodies determines the number of groups of factors, and all factors within a given chromosome tend to be linked in inheritance. Furthermore, Morgan was able to ascertain with approximate accuracy the point on the chromosome which a given factor occupies and in this way has made a very notable contribution to a knowledge of the structure of chromosomes and of living substance in general. The evidence on which these conclusions are based is somewhat involved and will be discussed in detail later. It is being gathered from many animals and plants beside the fruit fly and has now firmly established what was at first only a brilliant hypothesis as one of the important principles of inheritance.

PROBLEMS

Note.—In the summer squash, white fruit (W) is dominant over yellow (w); and "disc" fruit shape (D) is dominant over "sphere" shape (d).

31. In a cross between a squash plant homozygous for yellow fruit color and disc fruit shape and one homozygous for white fruit color and sphere fruit shape, what will be the appearance, as to color and shape of fruit, of the F_1? of the F_2? of the offspring of a cross of the F_1 back on the yellow disc parent? on the white sphere parent?

32. What are the gametes formed by the following squash plants, the genotypes of which for fruit color and shape are given; and what will be the appearance of the offspring from each cross?

$WW\ dd \times ww\ DD$	$Ww\ Dd \times Ww\ dd$
$Ww\ DD \times ww\ dd$	$Ww\ Dd \times ww\ dd$
$Ww\ Dd \times Ww\ DD$	$Ww\ Dd \times Ww\ Dd$

Note.—In the following six questions all of which deal with fruit color and shape in summer squash, the appearance of parents and offspring is stated. Determine in each case the genotypes of the parents.

33. White disc crossed with yellow sphere gives one-half white disc and one-half white sphere.

34. White sphere crossed with white sphere gives three-fourths white sphere and one-fourth yellow sphere.

35. White disc crossed with yellow sphere gives one-fourth white disc, one-fourth white sphere, one-fourth yellow disc, and one-fourth yellow sphere.

36. White disc crossed with white sphere gives three-eighths white disc, three-eighths white sphere, one-eighth yellow disc, and one-eighth yellow sphere.

37. Yellow disc crossed with white sphere gives all white discs.

38. White disc crossed with white disc gives 28 white disc plants, 9 white sphere plants, 10 yellow disc plants, and 3 yellow sphere plants.

39. A cross between a plant with white disc fruits and one with yellow sphere fruits gives 25 plants with white disc fruits, 26 with white sphere, 24 with yellow disc, and 25 with yellow sphere. If the white disc parent is self-fertilized, what proportion of its offspring will have yellow sphere fruits?

Note.—In guinea pigs, rough coat (R) is dominant over smooth coat (r); and black coat (B) is dominant over white (b).

40. Cross a homozygous rough, black animal with a smooth, white one. What will be the appearance of the F_1? of the F_2? of the offspring of

a cross of the F_1 back with the rough black parent? with the smooth white one?

41. In the F_2 generation in the preceding question, what proportion of the rough black individuals may be expected to be homozygous for both characters?

42. A rough, black guinea pig bred with a rough, white one gives 28 rough, black; 31 rough, white; 11 smooth, black; and 9 smooth, white. What are the genotypes of the parents?

43. Two rough, black guinea pigs when bred together have two offspring, one of them rough, white and the other smooth, black. If these same parents were to be bred together further, what offspring would you expect from them?

Note.—In Jimson weeds, purple flower color (P) is dominant over white (p); and spiny pods (S) over smooth (s).

44. A purple, smooth Jimson weed plant crossed with a white spiny one gives 320 purple, spiny and 312 purple, smooth. If these two types of offspring are bred together, what will *their* offspring be like, both as to appearance and genotypes?

45. Make the two following crosses in Jimson weeds: (1) homozygous purple, spiny with white, smooth, and (2) homozygous purple, smooth with white, smooth. Cross the F_1 of cross (1) with the F_1 of cross (2). What will be the appearance of their offspring?

Note.—In poultry, feathered legs (F) are dominant over clean legs (f); and pea comb (P) over single comb (p).

46. Two cocks, A and B, are bred to two hens C and D. All four birds are feathered-legged and pea-combed. Cock A with both hens produces offspring which are all feathered and pea. Cock B with hen C produces both feathered and clean, but all pea-combed; but with hen D produces all feathered but part pea-combed and part single. What are the genotypes of these four birds?

47. The offspring of a feathered-legged, pea-combed cock bred to a clean-legged, pea-combed hen are all feathered-legged. Most of them are pea-combed but some singles appear among them. What are the genotypes of the parents? What would be the offspring expected from a cross of this hen with one of her feathered-legged, single-combed sons?

48. In swine, white coat is dominant over black and the "mule-footed" condition over that with normal feet. A white, mule-footed boar, A, always produces white, mule-footed offspring, no matter to what sow he is bred. Another boar, B, however, also white and mule-footed, when bred to black sows produces about half white and half black offspring; and when bred to normal-footed sows, about half mule-

footed and half normal offspring. Explain this difference between these two animals by comparing their genotypes for these two traits.

Note.—In man assume that brown eyes (B) are dominant over blue (b); and right-handedness (R) over left-handedness (r).

49. A right-handed, blue-eyed man whose father was left-handed marries a left-handed, brown-eyed woman from a family in which all the members have been brown-eyed for several generations. What offspring may be expected from this marriage, as to the two traits mentioned?

50. A brown-eyed, right-handed man marries a blue-eyed, right-handed woman. Their first child is blue-eyed and left-handed. If other children are born to this couple, what will probably be their appearance as to these two traits?

51. A right-handed, blue-eyed man marries a right-handed, brown-eyed woman. They have two children, one left-handed and brown-eyed and the other right-handed and blue-eyed. By a later marriage with another woman who is also right-handed and brown-eyed, this man has nine children, all of whom are right-handed and brown-eyed. What are the genotypes of this man and his two wives?

Note.—In cattle the polled condition (P) is dominant over the horned (p); and in Shorthorns the heterozygous condition of red coat (R) and white coat (r) gives roan.

52. If a homozygous polled, white animal is bred to a horned, red one, what will be the appearance of the F_1? of the F_2? of the offspring of a cross of the F_1 back with the polled, white parent? with the horned red parent?

53. A polled roan bull bred to a horned white cow produces a horned, roan daughter. If this daughter is bred back to her father, what offspring may be expected as to horns and coat color?

Note.—In snapdragons red flower color (R) is incompletely dominant over white (r), the heterozygous condition being *pink;* and normal broad leaves (B) are incompletely dominant over narrow, grass-like ones (b), the heterozygous condition being intermediate in leaf-breadth.

54. If a red-flowered, broad-leaved plant is crossed with a white-flowered, narrow-leaved one, what will be the appearance of the F_1 and the F_2?

Note.—In garden peas, tall vine (T) is dominant over dwarf (t); green pods (G) over yellow (g); and round seed (R) over wrinkled seed (r).

55. If a homozygous dwarf, green, wrinkled pea plant is crossed with a homozygous tall, yellow, round one, what will be the appearance of the F_1? What gametes does the F_1 form? What is the appearance

of the F_2? What is the appearance of the offspring of a cross of the F_1 back on its dwarf, green, wrinkled parent? on its tall, yellow, round parent?

56. What will be the appearance of the offspring of the following crosses, in which the genotypes of the parents are given?

TT Gg Rr × *tt Gg rr*	*tt gg Rr* × *Tt Gg rr*
Tt GG Rr × *Tt Gg Rr*	*Tt Gg rr* × *tt Gg Rr*

In the following four questions, all of which concern garden peas, find the genotypes of the parents as to vine height, pod color, and seed shape:

57. A tall, yellow, round plant crossed with a dwarf, green, round one produces offspring three-eighths of which are tall, green, and round; three-eighths dwarf, green, and round; one-eighth tall, green, and wrinkled: and one-eighth dwarf, green, and wrinkled.

58. A tall, green, wrinkled plant crossed with a dwarf, green, round one produces offspring three-fourths of which are tall, green, and round and one-fourth of which are tall, yellow, and round.

59. A tall, green, round plant crossed with a tall, yellow, round one produces 26 tall, green, round offspring; 10 tall, green, wrinkled; 9 dwarf, green, round; and 3 dwarf, green, wrinkled.

60. A tall, yellow, round plant crossed with a dwarf, green, round one produces 58 tall, green, round offspring; 61 tall, yellow, round ones; 62 dwarf, green, round ones; 59 dwarf, yellow, round ones; 19 tall, green, wrinkled ones; 20 tall, yellow, wrinkled ones; 21 dwarf, green, wrinkled ones; and 20 dwarf, yellow, wrinkled ones.

61. In tomatoes, red fruit is dominant over yellow, two-loculed fruit, over many-loculed, and tall vine over dwarf. A breeder has pure races of red, two-loculed dwarf plants and of yellow, many-loculed, tall ones. He wants a race of red, many-loculed, tall plants. If he crosses his two races and raises an F_1 and an F_2, what proportion of this F_2 will be, in appearance, the type he desires? What proportion of these will be homozygous for all three characters? How can he determine which are the homozygous plants?

62. In poultry, the white plumage of Leghorns is dominant over colored plumage, feathered shanks over clean, and pea comb over single. If a homozygous white, feathered pea bird is crossed with a colored, clean, single one, what proportion of the white, feathered pea birds in the F_2 from this cross will breed true if mated to colored, clean, single birds?

63. In snapdragons normal flowers are dominant over peloric ones and tallness over dwarfness. Red flower color is incompletely dominant

over white, the heterozygous condition being pink. If a homozygous red, tall, normal-flowered plant is crossed with a homozygous, white, dwarf, peloric-flowered one, what proportion of the F_2 will resemble the F_1 in appearance?

64. If one individual is homozygous for four dominant factors and another for their four recessive allelomorphs, and if these two individuals are crossed, what proportion of the F_2 from this cross will resemble each parent, respectively, in appearance?

CHAPTER V

THE EXPRESSION AND INTERACTION OF FACTORS

Mendel's great contribution to genetics was the idea that the organism is an aggregation of separable units which are inherited in an orderly manner according to certain definite laws. The laws which Mendel himself framed, however, and which have been discussed in the preceding chapter, were based on the study of a few very simple cases of inheritance, and in presenting them the matter and the method of inheritance have been reduced to the simplest possible [illegible]ns. Later research soon discovered that the phenomena of heredity were by no means as simple as these particular examples were and that the principles which Mendel established are not sufficient to explain all the facts. These principles are, indeed, the firm foundation upon which all later research has built, but they have necessarily been qualified and extended to cover the ever-growing body of knowledge with regard to inheritance among all living things.

The conception of the individual as a group of unit factors, each producing a single invariable character and each entirely independent of the others, is far too simple, for experience has shown that the same factor often differs in its expression under different external or internal conditions and is much more complex than Mendel imagined it; and many factors, although *inherited* as independent units, are far from independent in their *expression*, but often interact upon one another in producing the actual bodily traits. Some of the complexities in the expression and interaction of factors will be discussed in this chapter, a few of the many cases which genetic investigation has established being taken as examples.

Differences in Dominance.—One of the most important influences in determining how a given factor shall express itself visibly in the body of an individual is its relation to the other member of the allelomorphic pair of which it forms a part. Mendel recognized in his principle of dominance that factors in a heterozygous condition did not contribute equally to the

characters of the individual produced. Geneticists have learned to recognize that dominance is not a simple thing, however, but that it occurs in varying degrees and is affected by various influences both inside and outside the organism.

Degrees of Dominance.—In most of the crosses which Mendel studied, dominance was essentially complete, all the heterozygous individuals exactly resembling one of the two parents, the other parent having no visible effect upon the hybrid offspring. Such complete dominance (or recessiveness), however, is not an attribute of all mendelian factors. There are many cases where dominance is *almost* complete. White Leghorn fowls, when crossed with colored races, produce offspring nearly pure white but which, nevertheless, betray their heterozygous condition by the presence of a few flecks of dark color. In many other cases dominance may be almost completely absent, and the two factors of an allelomorphic pair may contribute equally to the trait produced. Thus, as has been seen, a cross between red and white Shorthorn cattle results in neither red nor white offspring, but in an almost exactly intermediate condition called roan (Fig. 19), which will later segregate into red, roan, and white; and in Andalusian fowls a cross between black and splashed white produces the "blue" type of the breed, which will, in turn, produce black, blue, and white progeny (Fig. 32). Such characters as roan and blue are not due to factors in a homozygous condition (which produce such characters as red, black, and white) but to the interaction between two factors in a heterozygous condition; and hence they must always be "unfixable" and cannot be made to breed true. Instances where both factors find some expression, at least, in the heterozygous individual are probably more numerous than those of apparently complete dominance, so that we are justified in saying that many, perhaps most, characters in a heterozygote depend on a certain amount of interaction between the two members of the allelomorphic pair.

The Influence of Sex upon Dominance.—Furthermore, within the same factor-pair the degree of dominance displayed is not a fixed and constant thing but may sometimes vary radically, depending on a complex interaction with other conditions both within and without the organism.

Notable among these cases is the effect of sex upon the degree of dominance. Perhaps the best-known case of this is found in

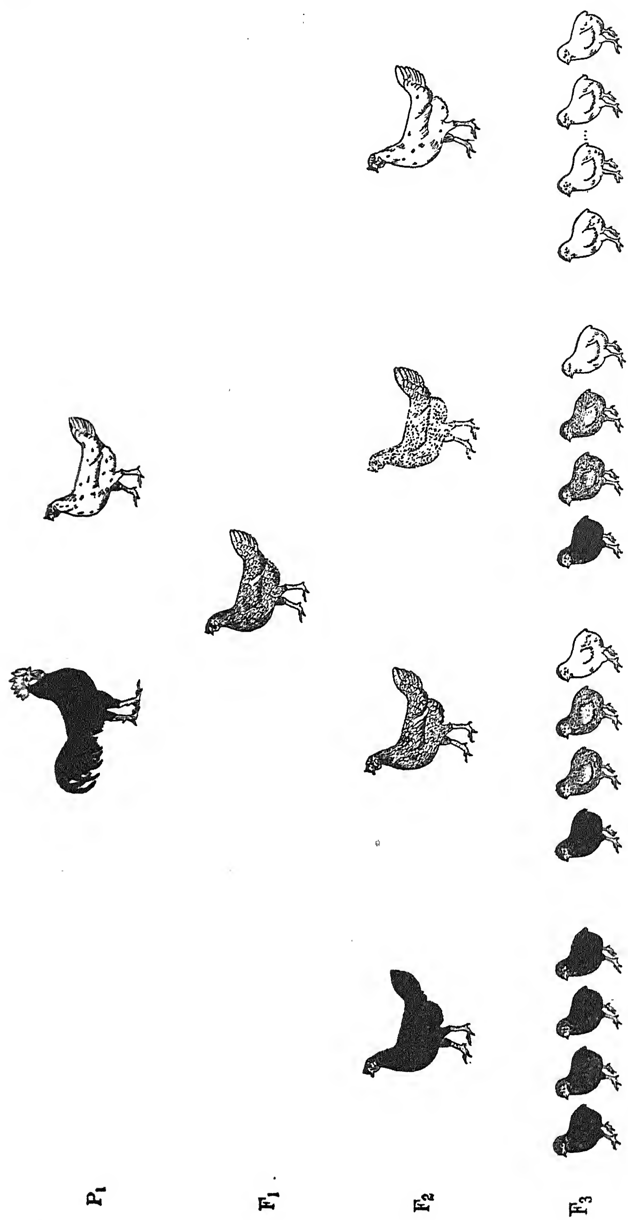


FIG. 32.—The inheritance of blue in Andalusian fowls. When black is crossed with splashed white all the F_1 birds are *blue*. These, if bred together, produce ¼ black, which breed true; ½ blue, which breed like the F_1 blue; and ¼ white, which breed true.

the inheritance of horns in sheep. The Dorset breed of sheep is horned in both sexes, while sheep of the Suffolk or Down breeds are hornless in both sexes. When these two types are crossed, reciprocally, the male offspring are all horned and the female all hornless. The horned condition is thus evidently dominant in males and recessive in females (Fig. 33). This conclusion is

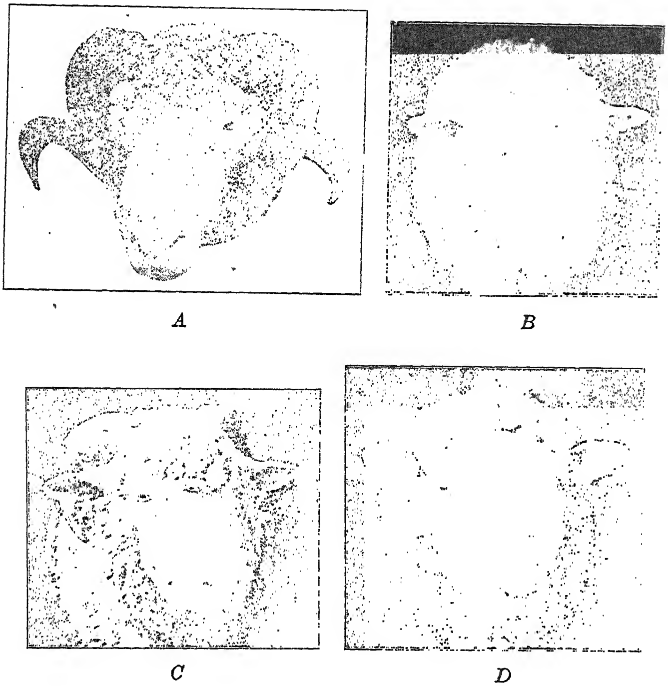


FIG. 33.—The inheritance of horns in sheep. *A*, horned Dorset male; *B*, hornless Southdown female; *C*, F_1 horned male, from cross of Dorset male with Southdown female; *D*, F_1 hornless female, from cross of Dorset male with Southdown female. The cross of horned by hornless produces F_1 horned males and hornless females, whichever way the cross is made. The horned character is dominant in the male and recessive in the female. (*Courtesy of the New Hampshire Agricultural Experiment Station.*)

further supported by a study of the F_2 generation, for if one of these F_1 (horned) males is bred to an F_1 (hornless) female, their offspring include both horned and hornless sheep. The proportions, however, are different in the two sexes, about three-fourths of the males being horned and one-fourth hornless; and about three-fourths of the females being hornless and one-fourth horned. Two factors for horns are necessary to produce a horned female,

and two for hornlessness to produce a hornless male. The heterozygous condition is horned in the males and hornless in the females.

A similar case of the dependence of dominance upon sex has been reported from an analysis of human pedigrees, which seem to indicate that baldness is a dominant trait in men and a recessive one in women, a circumstance which may account for the relatively greater frequency of bald individuals in the male than in the female sex.

In such cases as these it may be assumed that the degree of expression which is attained by a heritable factor is influenced in some way during the development of the individual by an internal secretion, or hormone, which is produced by the sex glands.

The Influence of the External Environment upon Dominance.—The degree of expression or dominance of a factor may also vary with the conditions under which the animal or plant develops. In the Jimson weed (*Datura*), for example, purple stem color seems to be completely dominant over green in plants which are grown out-of-doors during the summer. If these same types are grown in a greenhouse in the winter, the duration and intensity of the light are necessarily much reduced, and under these conditions the heterozygous purples may be distinguished from the homozygous ones by their paler color. The expression and consequently the degree of dominance of the factor for pigmentation, is evidently dependent in part upon light.

A somewhat similar case has been carefully studied in the fruit fly, *Drosophila*, except that here it is temperature rather than light which affects the degree of dominance. The normal compound eye of *Drosophila* is large and round, and consists of many facets or omatidia. One partially dominant factor has the effect of greatly reducing the number of facets and in producing a narrow type of eye known as bar eye. Another factor (ultra-bar) still further reduces the number of facets and is also partially dominant over full eye. When ultra-bar is crossed with normal, the heterozygote shows an intermediate number of facets, the number decreasing as the temperature under which the larvae are reared increases. A constant relation has been found to exist between temperature and the degree of dominance of this factor.

In addition to these cases in which the particular agency causing a reversal or alteration of dominance or factor expression

is known, there are many other instances in which dominance is variable, although the cause for this is as yet undiscovered.

Factor Interaction.—The variations and the irregularities in factor expression which have just been discussed are due to differences in the relationship between the two members of the *same* allelomorphic pair. There are many cases, however, in which factors belonging to *different* pairs, although inherited independently, may affect one another profoundly as they express themselves in the characteristics of the individual, so that a given trait often appears to depend not on a single independent unit factor but on an interaction between two or more of these. Some of the most notable complications in mendelian inheritance are due to such cases of factor interaction.

Combs in Fowls.—The first case of this kind was discovered a number of years ago by the English investigators Bateson and Punnett, during the course of experiments on the inheritance of comb form in fowls. Each of the common varieties of poultry possesses a characteristic type of comb. The Wyandotte breed, among others, has a low, regular, papillate comb known as the "rose" comb; Brahmas, and some of the varieties of game fowls have a narrower, higher, three-ridged comb known as the "pea" comb; while Leghorns and breeds of similar origin have "single" combs, consisting of a single, upright blade. Each of these types can be bred quite true (Fig. 34). Crosses made experimentally between rose-combed and single-combed varieties showed that rose was dominant over single and that there was a clear segregation into three-fourths rose and one-fourth single in the F_2. In

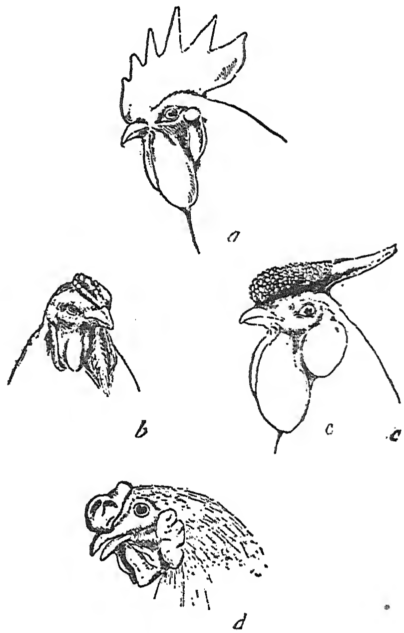


FIG. 34.—Four comb types of fowls. *a*, single; *b*, pea; *c*, rose; *d*, walnut. (*After Morgan.*)

crosses between pea-combed and single-combed birds, pea comb was also found to be dominant over single and a simple 3:1 ratio appeared in the F_2. A new and interesting result, however, was obtained when rose was crossed with pea, for instead of finding that either rose or pea appeared in the F_1, the experimenters were surprised to discover that neither of these usual comb types occurred in the hybrid but that the F_1 birds showed a new comb form different from either the rose or the pea. This was known as "walnut" comb from its resemblance to a half of a walnut meat, and had previously been noted as characteristic of the Malay breed of fowls, a race unrelated to the types from which the new walnut comb was obtained. When the F_1 walnut-combed birds were bred together, a still more remarkable result was manifest, for in the F_2 generation there appeared not only walnut-, rose-, and pea-combed fowls, but *single*-combed ones, as well. After large numbers of F_2 birds had been bred and classified, it was found that these types occurred in the following proportions: nine-sixteenths walnut, three-sixteenths rose, three-sixteenths pea, one-sixteenth single.

This was recognized as the ratio to be expected in F_2 from a cross of parents differing in *two* factors. The doubly dominant class in F_2 was apparently walnut, while the numbers of singles obtained indicated that this type contained both of the recessive factors involved, a conclusion supported by the fact that the F_2 singles when bred together produced only single-combed progeny in subsequent generations. The following explanation of these results was offered: The walnut comb depends on the presence of *two* dominant factors, R and P. One of these factors alone (R) produces the rose comb; the other alone (P) produces the pea comb. The combination of the recessive allelomorphs of these factors produces the single type of comb rp. These assumptions are illustrated in the diagram in Fig. 35.[1]

The similarity between the F_2 results in this diagram and the common two-factor case explained on page 67 will be readily noticed. The mode of inheritance of the factors for rose and pea does not differ at all from the usual mendelian scheme, for they

[1] The checkerboard scheme in this diagram, which is similar to that employed in the study of a simple dihybrid, is a useful means of finding the various genotypes resulting from combinations of the gametes formed by complex heterozygotes of this sort. The relative proportions of the different types of individuals to be expected may be read off directly.

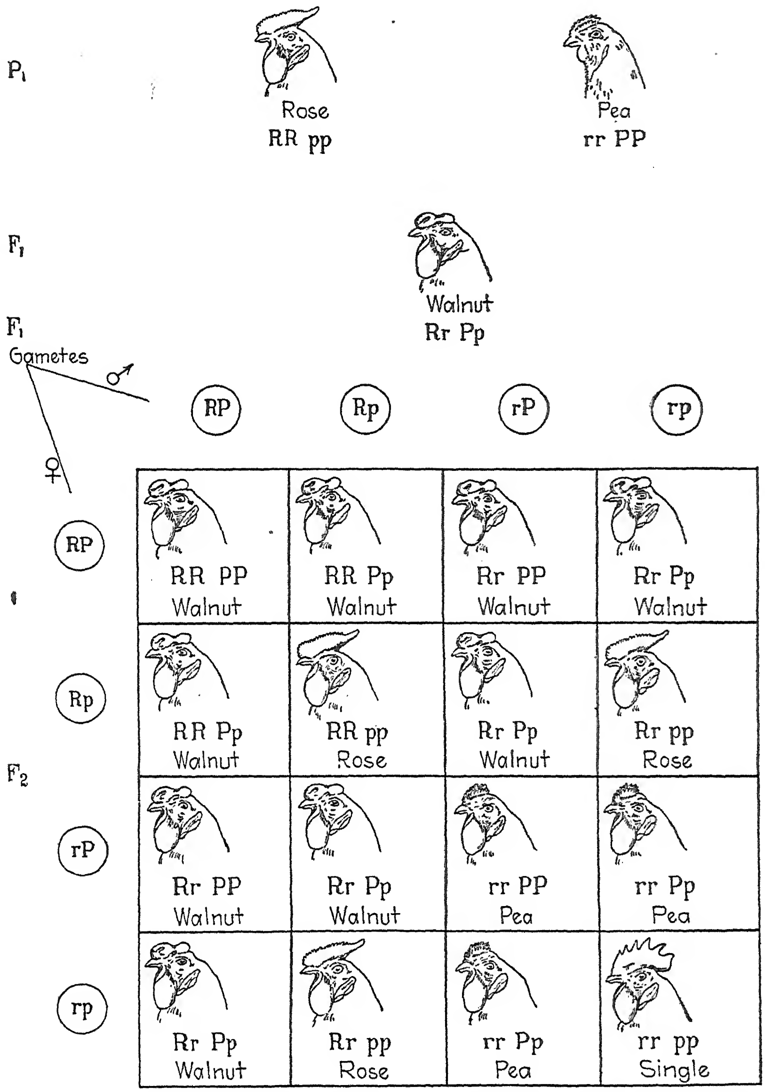


FIG. 35.—Diagram showing interaction of factors for comb form in fowls. The cross of a pure rose-comb bird with a pure pea-comb one gives all walnut-combed offspring. The 16 possible combinations of the F_1 gametes, with their genotypes and the phenotypes resulting from factor interaction, are shown in the F_2 checkerboard.

display complete independence of assortment. The differences which distinguish this and similar cases from ordinary dihybrid inheritance are that (1) the F_1 resembles neither parent, and (2) *two new types* appear in F_2. One of these new characters (walnut comb), therefore, evidently results from an interaction between two independently inherited dominant factors, while the other (single comb) results from the interaction of their two recessive allelomorphs. These peculiarities are not due to a new method of inheritance but simply to the circumstance that both factors involved happen to express themselves in the same part of the organism, in this case the comb.

Flower Color in Sweet Peas (the 9:7 Ratio).—A similar type of interaction has been found between two factors affecting flower color in the sweet pea. This plant occurs in a number of true-breeding varieties, most or all of which are descended from the wild sweet pea of Sicily, which bears a purple flower with red wings. While studying a number of the different cultivated varieties, Bateson and Punnett found that purple flower color is dominant over white and gives a typical 3:1 ratio in the F_2. They also observed that the white types bred true, as was to be expected, and that crosses between white varieties usually produced white-flowered progeny. In one instance, however, where two pure white varieties were crossed, there resulted quite unexpectedly no white offspring at all, but only *colored-flowered* plants. The flowers of these F_1 hybrids were very similar in color to the wild Sicilian ancestor of the cultivated sweet pea. When such purple-flowered F_1 plants were self-fertilized, they produced an F_2 generation consisting of about nine-sixteenths purple-flowered plants and seven-sixteenths white-flowered ones. All of the F_2 white individuals bred true when self-fertilized. The purples, however, were evidently of several different types, for a few bred true; others produced colored- and white-flowered plants in the proportion of three-fourths colored to one-fourth white; while still others produced offspring of which about nine-sixteenths were colored and seven-sixteenths white.

This result, like the inheritance of comb shape, may also be explained on the basis of two independent factor-pairs, but the type of interaction between them is somewhat different, for no new traits appear in the F_1 or F_2. The fact that purple flower color occurs in nine-sixteenths of the F_2 plants suggests

that it appears only when two independent dominant factors are present together, and that it results from some sort of interaction between them. White flower color may thus evidently be due to the absence of either or both of these factors. Denoting one of the factors by C (color) and the other by P (purple), it may be assumed that one white parent was of the genotype $CC\ pp$ while the other was $cc\ PP$. Neither the color factor alone nor the purple factor alone is, by this assumption, able to cause

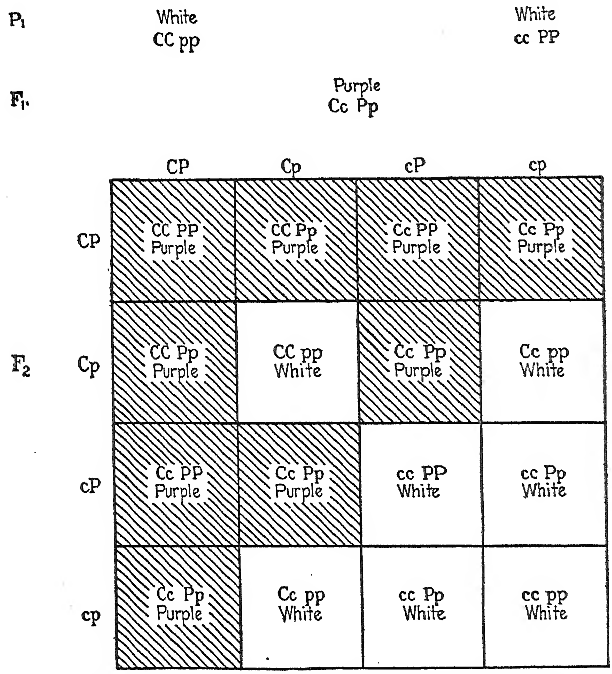


FIG. 36.—The 9:7 ratio. Checkerboard showing the expected composition of the F_2 from a cross of two white-flowered sweet peas which produce all purple-flowered plants in F_1.

the production of color in the flowers. The cross between two such white types produces the heterozygote $Cc\ Pp$ which bears colored flowers, since it contains both the factors for color and purple. When this hybrid forms its gametes, the factors C and P segregate independently, and the gametes formed may be written CP, Cp, cP, and cp. The combinations between these types of gametes and the resulting flower colors of the F_2 plants are shown in the checkerboard diagram in Fig. 36. The

total number of plants containing both C and P is nine; the number containing either one alone, or neither, is seven. This agrees with the proportion of colored and white plants actually found (nine-sixteenths and seven-sixteenths).

The ratio here is obviously the normal 9:3:3:1 expected in F_2 when the parents differ in two factors, but with the last three terms added together (9:7). The peculiarity of this ratio arises from the fact that *all* plants which lack either factor are white, regardless of the condition as to the other factor. Thus three F_2 plants are white because they lack the color factor; three are white because they lack the purple factor; while one white lacks both of these.

A study of the genotypes of the plants with colored flowers also explains why they breed so differently in later generations. One of them (with the genotype $CC\,PP$) breeds true to purple. Four (with the genotypes $Cc\,PP$ or $CC\,Pp$) produce about three-fourths purple and one-fourth white offspring when inbred, since they are homozygous for one of the factors. Four others (with the genotype $Cc\,Pp$) produce nine-sixteenths purple and seven-sixteenths white, just as did the F_1. Such factors as C and P, which are similar in their individual effect but are both necessary to the production of another and different character are called *complementary* factors. In the sweet pea, again, the complications are due not to any change in the principles of inheritance but to (1) the dependence of one factor on another and (2) the expression of two different factors in the same part.

The interaction of two factors such as C and P to produce a character quite different from that which results from either one alone may perhaps be made more clear if a simple comparison with certain chemical phenomena is used. It is well known that when a colorless solution of an alkali (such as KOH) and a colorless solution of an "indicator" (such as phenol-phthalein) are brought together, a light red color appears. Here the chemical interaction of two colorless substances results in the production of color. The alkali may be compared to the material, whatever it is, which is furnished by the factor C and the indicator to that furnished by the factor P.

This illustration may be more than mere analogy with a chemical process, for a study of the chemistry of pigment production in plants lends much support to the idea that color does actually depend on a union of two (or more) different chemical

substances. In sweet peas and some other plants it is supposed that two colorless substances, one of which acts as a *chromogen* or color base, the other as a color developer or activator (an enzyme), are concerned in pigment production. A simple explanation of the sweet pea case is that one white race contains the chromogen (the *C* factor), while the other contains the enzyme or activator (the *P* factor). The identification of a chemical substance with a genetic factor has been made in a few cases with a reasonable degree of probability.

Reversion.—The method of inheritance of flower color in sweet peas suggests an explanation for the numerous instances among domesticated animals and plants in which crosses between true-breeding varieties produce progeny resembling a remote ancestor more than they do either parent. Plant and animal breeders have noted these peculiar "throwbacks" or "reversions" for many years, but in the absence of any satisfactory explanation they have regarded reversion as the expression of some mysterious force which caused the retention and subsequent reappearance of a remote ancestral trait. It is now known that such reversion may be explained in terms of ordinary mendelian inheritance, for the reappearance of an old trait is usually due to the reunion of the two or more factors necessary for its production, which had become separated in the history of the plant or animal. Thus, in the sweet pea, it is plain from the experiment cited above that purple flower color depends on at least two factors, and that white flower color results when either is absent. It is easy to imagine that one white variety arose when the purple type lost one of these factors, such as factor *C* by mutation; while the second white variety arose from the loss of the other factor, *P*. Thus the two elements necessary for purple color became separated into two different strains. When these strains were crossed, the two complementary factors essential for the production of purple flowers were reunited, and the primitive or "reversionary" flower color appeared. A similar case of reversion in rabbits is shown in Fig. 37.

Coat Color in Rodents (the 9 : 3 : 4 Ratio).—A similar but more complex case of factor interaction and reversion has been worked out in breeding experiments with "fancy" varieties of the common house mouse, where not only two but a number of factors have been found to interact in producing what appears to be a simple character. The ancestral or original coat color of this species is seen in Supplimentary factors.

FIG. 37.—Reversion in rabbit coat color. A cross between two different varieties of white rabbits, top and bottom, produces all gray young like the wild type, center. (*From Castle, in Journal of Heredity.*)

the grayish-brown or grizzled pattern of our ordinary wild mice. When closely examined, this is found to be due to the presence of two pigments in the fur. The individual hairs are for the most part black with a narrow yellow band near the tip. Brown

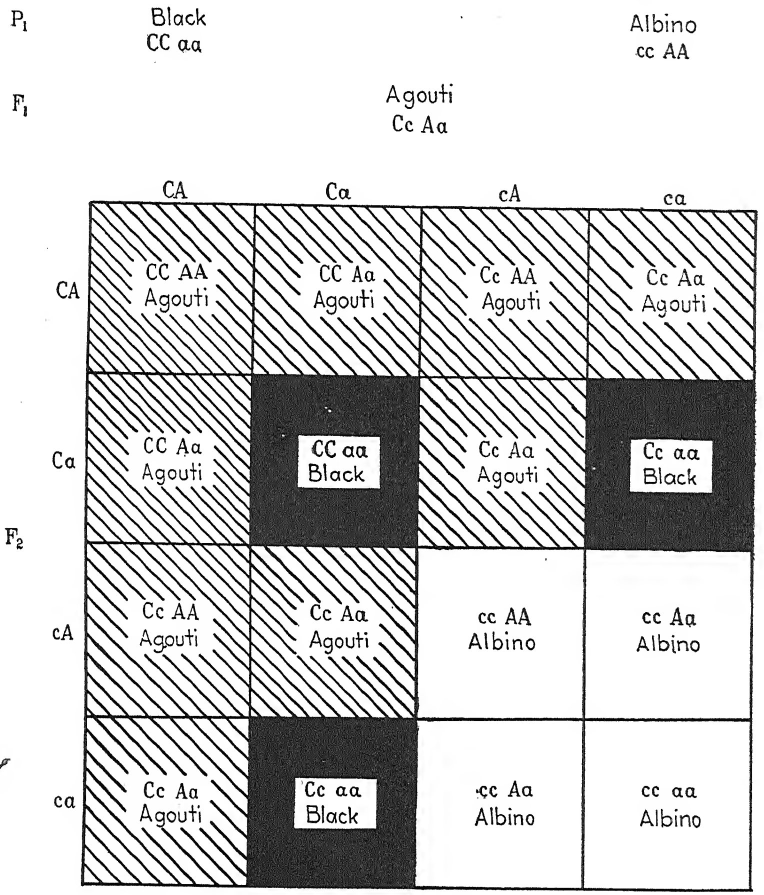


FIG. 38.—The 9:3:4 ratio. Checkerboard showing the expected composition of the F_2 from a cross of black and albino mice, which produce all agouti animals (wild type) in F_1.

pigment is also visible in the hairs when viewed through a microscope. The under side of the animal is usually much lighter, the hairs being cream or yellow, with some black or gray at the base. This inconspicuous and hence protective coloration, which is known as the "agouti" pattern, characterizes nearly all of

the wild rodents, such as the Norway rat, the wild rabbit, the guinea pig, the gray squirrel, and many others.

A number of variations which have taken place in this wild gray or agouti coat coloration have been preserved under domestication and have given rise to the many color varieties of mice known to fanciers. The commonest and most familiar variation is the albino, in which the coat is white and the eyes are pink or blood color because of the entire absence of pigment from the iris. Albinos always breed true, and this variation has been found to behave as a simple recessive to any color. Another variation in coat color probably arose through the disappearance of all yellow pigment from the agouti pattern, leaving the fur solid black. Black is recessive to the wild gray type and breeds true. When black mice are crossed with ordinary albinos, the progeny are usually *all agouti* like the wild type. When these F_1 agoutis are inbred, their progeny consist, on the average, of nine-sixteenths agouti animals, three-sixteenths black, and four-sixteenths albino (Fig. 38). This, like the 9:7 ratio encountered in sweet peas, apparently indicates a difference of two factors in the parents. Here, however, the last two terms of the ordinary 9:3:3:1 ratio have been added together, indicating that two of the ordinarily different classes of the dihybrid F_2 zygotes cannot be distinguished. The results are explained on the assumption that the parents differ in (1) a factor, C, necessary for the development of any color, which the black mice contain but which is lacking in the albinos, and in (2) a factor for the agouti pattern, A, which results in a banding of the black hairs with yellow. Since the black mice cannot contain this factor A (or they would appear agouti), it must have come from the albino parent, where, in the absence of the ability to develop any color at all it could have no visible expression. The recombination of these two factors, one for color and the other for the agouti pattern, reconstitutes the genotype of the wild mouse, and a "reversionary" type results.

This case is, therefore, similar to that of flower color in sweet peas in that (1) two independently inherited factors both affecting the same part (in this case coat color) interact to produce a single character; and (2) this interaction produces reversion in the F_1 generation, followed by the reappearance in the F_2 of both of the parental colors as well as the reversionary type. It differs somewhat from the previous case, for in sweet peas

three of the F_2 genotypic classes have the same appearance, producing a 9:7 ratio, whereas in mice only *two* of the F_2 genotypic classes are indistinguishable, thus producing a 9:3:4 ratio. Both of these are modifications of the 9:3:3:1 ratio normal for a dihybrid.

In mice it is probable that the mechanism of factor interaction and reversion is also chemical in nature, for it is supposed that albinos, although lacking the chromogen or color base, retain factors for the enzymes or activators necessary for developing the various colors; while colored varieties probably all retain the color base, but in combination with different enzymes. Albinos then may be thought of as undeveloped negatives, to which the color developer from various colored races must be added for complete expression of the factors which they carry.

Analysis of Coat Color in Mice.—In house mice, moreover, a large number of spontaneous variations have provided the opportunity for a thorough genetic analysis of the factors affecting coat color. A dozen such factors have been studied and their interrelationships made out. *C* is the fundamental color factor, necessary for the production of any pigment in the coat. Another factor, *A* as we noted, determines the development of the agouti, gray, or grizzled pattern. Its recessive allelomorph, *a*, is present in all non-agouti mice, such as blacks or browns. Still another, *B*, governs the development of black pigment, and is dominant over its allelomorphic condition of brown or chocolate, *b*. Many varieties are spotted with white in a blotched or piebald pattern, and such mice contain a factor, *s*, which is recessive to self or solid color, *S*. Another factor, *d*, brings about a clumping of the black and brown pigment granules in the hairs and makes these colors appear faded or *dilute*, as opposed to the normal fully pigmented form, *D*. Another factor reduces the amount of black and brown pigment in the fur, giving it a pale and washed-out appearance, and also reduces the pigment in the iris, making the eyes appear reddish or pink like the eyes of albinos. This factor, which is called pink eye (*p*) from its most noticeable effect, is recessive to the normal dark-eyed, intense-colored condition, *P*. These factors all segregate sharply and may occur in any combination. There is also a dominant factor for yellow, which will be discussed later. Some of these combinations result in characters which are quite distinctive and have been given names of their own. Thus the

non-black agoutis are called "cinnamon," the dilute blacks "blue," the dilute browns "silver fawn," and so on. A table with these various factor combinations, together with the type of coat color produced by each, is presented below.

TABLE V.—INTERACTION OF FACTORS FOR COAT COLORS IN MICE

Factors						Gametic formula	Phenotype
				P	*S*	*CABDPS*	Wild type agouti
			D		*s*	*CABDPs*	Spotted agouti
				p	*S*	*CABDpS*	Pink-eyed agouti
		B			*s*	*CABDps*	Pink-eyed spotted agouti
				P	*S*	*CABdPS*	Dilute agouti
			d		*s*	*CABdPs*	Spotted dilute agouti
				p	*S*	*CABdpS*	Pink-eyed dilute agouti
	A				*s*	*CABdps*	Pink-eyed spotted dilute agouti
				P	*S*	*CAbDPS*	Cinnamon
			D		*s*	*CAbDPs*	Spotted cinnamon
				p	*S*	*CAbDpS*	Pink-eyed cinnamon
		b			*s*	*CAbDps*	Pink-eyed spotted cinnamon
				P	*S*	*CAbdPS*	Dilute cinnamon
			d		*s*	*CAbdPs*	Spotted dilute cinnamon
				p	*S*	*CAbdpS*	Pink-eyed dilute cinnamon
C					*s*	*CAbdps*	Pink-eyed spotted dilute cinnamon
				P	*S*	*CaBDPS*	Black
			D		*s*	*CaBDPs*	Spotted black
				p	*S*	*CaBDpS*	Pink-eyed black
		B			*s*	*CaBDps*	Pink-eyed spotted black
				P	*S*	*CaBdPS*	Dilute black
			d		*s*	*CaBdPs*	Spotted dilute black
				p	*S*	*CaBdpS*	Pink-eyed dilute black
	a				*s*	*CaBdps*	Pink-eyed spotted dilute black
				P	*S*	*CabDPS*	Brown
			D		*s*	*CabDPs*	Spotted brown
				p	*S*	*CabDpS*	Pink-eyed brown
		b			*s*	*CabDps*	Pink-eyed spotted brown
				P	*S*	*CabdPS*	Dilute brown
			d		*s*	*CabdPs*	Spotted dilute brown
				p	*S*	*CabdpS*	Pink-eyed dilute brown
					s	*Cabdps*	Pink-eyed spotted dilute brown
c	with any other factors					*c*........	Albino

All of these types, except yellow, are recessive to the wild coat and appear to have arisen from it by the loss or change of one or more factors. Thus at any time the wild type may be reconstituted by bringing into combination all of the allelomorphs of the factors which are responsible for these new types. *In fact, the wild coat color itself is found to depend on the presence and interaction of all of the factors named.* Thus, in order to produce the agouti pattern there must be present the factors for color (C), agouti (A), black (B), dark eye (P), dense color (D), solid color (S), and non-yellow (y). With regard only to these factors the genotype of the wild mouse may be written $AA\ BB\ CC\ DD\ PP\ SS\ yy$.[1] The factors named do not include all which are known, nor is it believable that more than a small sample of the factors affecting coat color in mice have been studied. Were knowledge complete, it is probable that the list of factors necessary for the production of the agouti pattern would be much longer and that the letters of the alphabet would be exhausted in attempting to write the genotype of the wild mouse. Here, then, is a clear and convincing example of factor interaction. In order that the apparently simple pattern characteristic of wild house mice may be developed, there must be present at least seven factors (probably many more) each of which has a definite effect on coat color. If any single factor is missing or changed, a coat pattern differing more or less widely from the wild type results.

This type of factor interaction is not exceptional, but is found wherever numerous variations in a single aspect of the organism are carefully analyzed. Such analyses have been made for several groups of characters in corn, the plant which has been most thoroughly studied genetically. More than a dozen factors affecting the color of the plant are known. The normal color is green which, like the agouti pattern of mice, results from the combined action of the allelomorphs of all of these factors. If one factor is missing, the plant is white instead of green; if another drops out or changes, the leaves become red or purple in the sun; whereas absence of various other factors produce brown, yellow, and various combinations of these colors in striped or blotched patterns. In fact, it may be accepted as a

[1] These factors all show essentially complete dominance, so that their heterozygous condition will give the same result as is produced by the homozygous form here given. Thus an animal with the genotype $Aa\ Bb\ Cc\ Dd\ Pp\ Ss\ yy$ would also be agouti in appearance.

general rule that the characters of a plant or animal depend on multiple and finely balanced interactions between a very large number of factors.

Epistasis.—One of the first complications which was encountered in the discussion of unit inheritance was the fact of dominance, by which the presence of one factor was obscured or hidden through the action of its dominant allelomorph. It sometimes happens that when two different factors, which are not allelomorphs, both affect the same part or trait of the organism, the expression of one factor covers up or hides the expression of the other. A factor which thus masks or prevents the expression of another is said to be *epistatic* to it, and the factor which is hidden is said to be *hypostatic*. This covering up of one factor by another is known as *epistasis*, and is similar to dominance except that it occurs between different factors instead of between the two members of an allelomorphic pair.

In Squashes (the 12:3:1 *Ratio).*—An example will serve to make this distinction clear. In summer squashes there are three common fruit colors, white, yellow, and green. In crosses between white and yellow, and between white and green, white is always found to be dominant; and in crosses between yellow and green, yellow is always found to be dominant. Yellow thus acts as a recessive in relation to white but as a dominant in relation to green. There is evidently a factor for white, W, which is epistatic to those for yellow and green; and so long as it is present, no color will be produced in the fruit, regardless of whether factors for color are present or not. Where this factor for white is lacking, however (in plants which are ww), the fruit color will be yellow if the factor for yellow, Y, is present and green if it is absent. Green-fruited plants may thus be represented by the double recessive genotype $ww\,yy$; yellow-fruited plants by $ww\,YY$, and white-fruited ones either by $WW\,YY$ or $WW\,yy$.

The truth of this assumption that there are two independent factor-pairs, one epistatic over the other, may be tested by crossing a homozygous white from a race which is known to carry yellow, $WW\,YY$, with a green, $ww\,yy$. Here the F_1 plants, $Ww\,Yy$, are white-fruited. They should produce four types of gametes, WY, Wy, wY, and wy, and the F_2 expected from a cross between two such F_1 plants is indicated in the checkerboard (Fig. 39).

Three-fourths of the plants in this generation will evidently carry *W* and will thus appear white-fruited no matter what the rest of the genotype may be. Of the one-fourth which have no

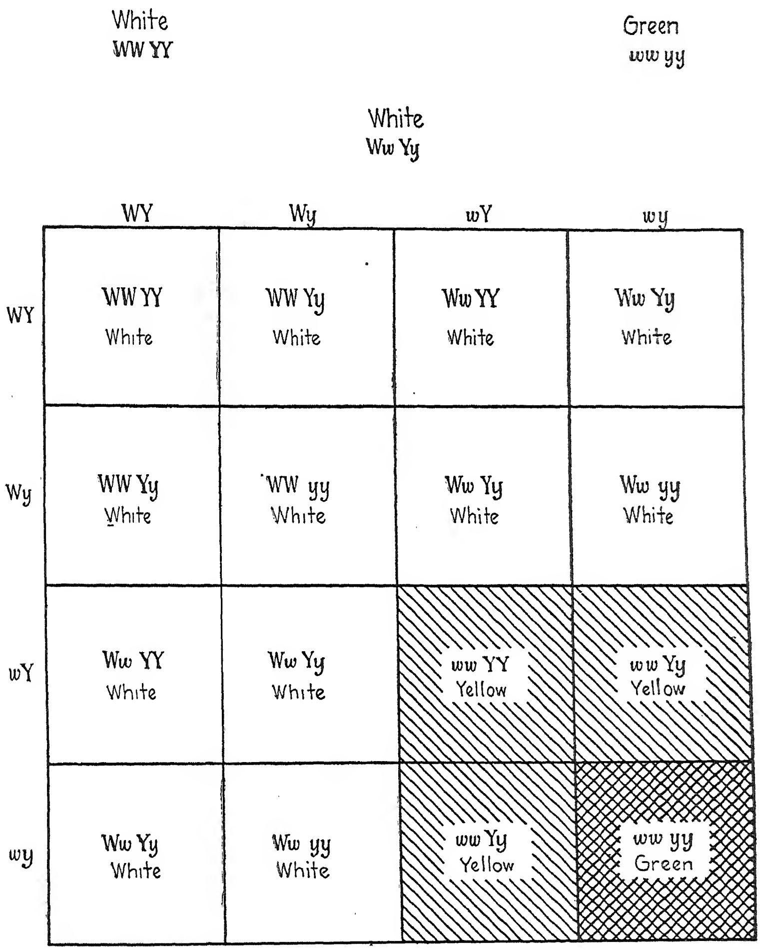


FIG. 39.—The 12:3:1 ratio. Checkerboard showing the expected composition of the F_2 from a cross of a white-fruited squash plant which carries yellow, with a green-fruited one.

factor for white, however, three-fourths, or three-sixteenths of the whole, will carry yellow and thus appear yellow; and one-fourth, or one-sixteenth of the whole, will not, and will thus appear green. The occurrence of white, yellow, and green in

the F_2 in approximately the ratio expected on the assumption (12:3:1) is actually realized in breeding experiments. The essential fact here is that the white factor masks everything which is hypostatic to it, so that the factor for yellow, which segregates quite independently of white, produces a visible effect only in that fraction of the F_2 which lacks the white factor.

In Poultry (*the* 13:3 *Ratio*).—Another interesting example of epistasis may be cited from poultry. It has already been noted that the white plumage of White Leghorn fowls is almost completely dominant over the colored plumage of black, barred, or other colored varieties. The white plumage of some other white varieties, however, such as White Wyandottes, or White Plymouth Rocks, has been found to be *recessive* to colored plumage and to be due to a factor distinct from that which produces the white of Leghorns. It is assumed that the recessive white varieties of fowls, like albino rodents, are white because they lack a factor for some color base or chromogen; but that the dominant white of Leghorns, on the contrary, is due to a factor which prevents or inhibits the development of color in the plumage. Experiment shows that White Leghorns do contain a color factor and with it a factor which inhibits its expression. They are genetically colored birds which are unable to develop their true color. Denoting such an inhibiting factor by I and the color factor by C, the White Leghorn is $II\ CC$ and the White Wyandotte is $ii\ cc$. A test of this hypothesis by crossing White Leghorns with White Wyandottes produces a curious result. The F_1 chickens from such a cross are white with small dark flecks and resemble the F_1 birds produced by crossing White Leghorns with colored fowls. When these F_1 whites are bred together, however, white *and colored* chicks appear in F_2 in the proportion of about thirteen-sixteenths white (or white with small dark flecks) to three-sixteenths colored. Although this ratio is not like that of any of the other two-factor ratios which have been discussed (9:3:3:1, 9:7, 9:3:4, and 12:3:1), it may be explained in the same way as these with the additional assumption that the inhibiting factor I is epistatic to or hides the segregation of the color factor C.

On the assumption made, the F_1 fowls from the cross of dominant white by recessive white should be of the genotype $Ii\ Cc$ and should form gametes IC, Ic, iC, and ic in equal numbers. When F_1 fowls are bred together, these gametes should recom-

bine at random, producing the genotypes shown in the checkerboard (Fig. 40).

In determining the appearance of these F_2 chickens, it should be remembered that wherever I is present, pigment development is inhibited, so that fowls which inherit I are white, what-

P_1 White (Leghorn) II CC — White (Wyandotte) ii cc

F_1 White Ii Cc

F_2

	IC	Ic	iC	ic
IC	II CC White	II Cc White	Ii CC White	Ii Cc White
Ic	II Cc White	II cc White	Ii Cc White	Ii cc White
iC	Ii CC White	Ii Cc White	ii CC Colored	ii Cc Colored
ic	Ii Cc White	Ii cc White	ii Cc Colored	ii cc White

FIG. 40.—The 13:3 ratio. Checkerboard showing the expected composition of the F_2 from a cross of a variety with dominant white plumage and one with recessive white plumage, in fowls.

ever other factors they may receive. There are twelve such types among the sixteen shown in the F_2 checkerboard. The segregation of the *Cc* pair, which determines the presence or absence of color can, therefore, be observed only in those four types, among the sixteen, which do not receive I. Of these,

three should receive C and be colored (shaded on the checkerboard), and one should not receive C and should, therefore, be white. Although of a different genotype from the other whites, this single cc chicken is indistinguishable from them except by a breeding test. In appearance, then, thirteen out of every sixteen F_2 chickens should be white and three colored; and the actual results are in close accord with this expectation. The peculiarity in this case, it should be noted, lies again in the ability of the dominant white factor I to mask the segregation of the Cc pair.

The complications introduced by epistasis are comparable with those produced by dominance, i.e., two or more genotypes are indistinguishable in appearance. In cases of epistasis, however, there are always two or more factors involved, each of which affects the same part of the organism. This same condition occurred in cases of interaction such as that observed in comb shape in fowls, but in these latter *both* factors are expressed, producing a new or different condition of the part. In epistasis, on the contrary, the competition of two factors for expression in one part results in the apparent triumph of one and the suppression of the other, so that the original traits are recovered but in modified ratios.

Duplicate Factors.—In the last few cases cited the two interacting or competing factors, although affecting precisely the same part or trait of the individual, were clearly different and distinguishable in their effects. Thus in comb form one of the interacting factors when alone produces a pea comb which is quite different from the rose comb formed by the other. A number of cases have come to light, however, in which two or more factors not only affect the same trait but affect it in precisely the same way. Such factors, which have the same or nearly the same expression, are known as *duplicate* factors. Their discovery has pointed the way to an explanation of some of the most complicated cases of inheritance.

In Bursa (the 15:1 Ratio).—One of the simplest instances of duplicate factors is involved in the inheritance of capsule or pod form in the shepherd's purse (*Bursa*) as reported by G. H. Shull. One race of this species has characteristically triangular capsules, whereas in another they are ovoid or top-shaped. When these two types are crossed, the F_1 plants all have triangular capsules, the dominance of this shape being complete. In the F_2, however,

there are ordinarily found to be about fifteen plants with typical triangular capsules to every one with ovoid capsules. This F_2 ovoid plant breeds true in subsequent generations, whereas of the F_2 triangular plants some breed true, others produce triangular and ovoid plants in the ratio of 3:1, and others produce these types in the ratio of 15:1. Remembering that where parents differing in two factors are crossed, the double recessive type appears in only one-sixteenth of the F_2 progeny (as opposed

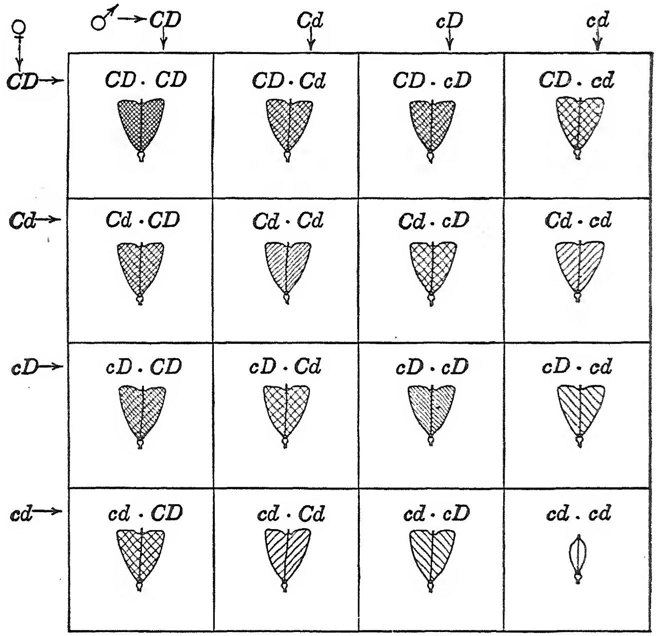


FIG. 41.—The 15:1 ratio. Checkerboard showing the expected composition of the F_2 from a cross between a type of shepherd's purse (*Bursa*) with triangular capsules (homozygous for two duplicate factors) and a type with top-shaped capsules. (*After G. H. Shull.*)

to one-fourth in a single-factor cross), the hypothesis at once suggests itself that the triangular capsule of *Bursa* is caused by two dominant duplicate factors or by either one of them alone, and that the ovoid type is due to the absence of both of these. The 15:1 ratio is thus still another modification of the 9:3:3:1 ratio, the first three terms here being indistinguishable from each other. Representing these two factors for triangular capsule by C and D, the genotypes and phenotypes of the F_2 may be represented by the checkerboard in Fig. 41.

The hypothesis of duplicate factors not only explains this peculiar ratio but makes it easier to understand the differences in breeding behavior which have been found to exist between the various triangular types occurring in F_2. Seven plants out of sixteen (those which are homozygous for either C or D or both) should breed true to triangular capsules in later generations. Four plants have only one of the triangular factors represented and that in a heterozygous condition ($Cc\ dd$ or $cc\ Dd$), so that these plants may be expected to produce offspring about three-fourths of which have triangular capsules and one-fourth ovoid ones. The remaining four are heterozygous for both factors ($Cc\ Dd$) and should thus produce offspring, when inbred, in about the ratio of 15:1, just as does the F_1 hybrid. These expectations have been borne out by actual breeding tests.

In Wheat.—A somewhat more involved case was brought to light during some breeding experiments on wheat by the Swedish investigator Nilsson-Ehle. He found that the red color of the grain in certain varieties was dominant to the white or colorless condition of the grain in other varieties. After red and white races had been crossed, however, these colors appeared in various ratios in the F_2 generations. From some crosses he obtained a normal one-factor ratio of three-fourths red to one-fourth white. In other F_2 counts, however, the ratio was apparently fifteen red to one white, and in still others sixty-three red to one white. By comparison with the shepherd's purse it may be inferred that the red color may be due to the operation of one, of two, or even of three independent factors, any one of which, or all together, may produce the color; and that white is due to the absence of all of these. Breeding tests show that the red plants which, when crossed with white, produce a ratio of three red to one white in the F_2 do indeed possess but a single factor-pair for red; whereas the reds which give the 15:1 and the 63:1 ratios possess two and three factor-pairs for red, respectively.

Denoting these various factors for red by R_1, R_2, and R_3, we may represent the results of crosses by checkerboards as before. A cross of "double red" and white is shown in Fig. 42.

According to the assumption, the presence of a single factor for red (either R_1 or R_2) is sufficient to cause the development of red color in the grains. Fifteen of the F_2 types in the checkerboard have either R_1 or R_2 and should be red, while only one out of the sixteen has neither, and this is the double recessive white

plant. The cross of a "triple red" with a white can be shown in the same way, with the appearance of the white plant in the F_2 expected only once in every sixty-four individuals.

In this example it is significant that red is not completely dominant over white, for plants in which there are two red factors have darker grains than those with one; plants with three are darker than those with two, and so on, which indicates that

P_1 — $R_1R_1\ R_2R_2$ Red × $r_1r_1\ r_2r_2$ White

F_1 — $R_1r_1\ R_2r_2$ Red

F_2		R_1R_2	R_1r_2	r_1R_2	r_1r_2
	R_1R_2	$R_1R_1\ R_2R_2$ Red	$R_1R_1\ R_2r_2$ Red	$R_1r_1\ R_2R_2$ Red	$R_1r_1\ R_2r_2$ Red
	R_1r_2	$R_1R_1\ R_2r_2$ Red	$R_1R_1\ r_2r_2$ Red	$R_1r_1\ R_2r_2$ Red	$R_1r_1\ r_2r_2$ Red
	r_1R_2	$R_1r_1\ R_2R_2$ Red	$R_1r_1\ R_2r_2$ Red	$r_1r_1\ R_2R_2$ Red	$r_1r_1\ R_2r_2$ Red
	r_1r_2	$R_1r_1\ R_2r_2$ Red	$R_1r_1\ r_2r_2$ Red	$r_1r_1\ R_2r_2$ Red	$r_1r_1\ r_2r_2$ White

FIG. 42.—Diagram showing the result of a cross between a red-kernelled and a white-kernelled wheat, where the red color is due to the operation of either or both of two factors, R_1 and R_2.

these duplicate factors have *cumulative* effects. This conception, through its extension in the theory of multiple factors, has a very important bearing on the modern explanation of the inheritance of quantitative or size characters, a subject which is one of the recent important developments in genetics and which will be treated in detail in a later chapter. The important point to be emphasized in the present connection, however, is that the same effect may be produced by several different

factors which are inherited quite independently of one another in typical mendelian fashion.

Modifying Factors.—Of the several factors which interact to produce a given effect, one may appear to determine the presence of some character, such as a certain eye color or a white-spotted coat, while other distinct and separable factors may affect the degree of development of this character, or otherwise *modify* the expression of the chief factor. In mice solid- or self-colored coat behaves as a single factor dominant to white-spotted piebald coat. White spotted mice may have much or little spotting, and the variation is practically continuous from a self-colored coat with a small white spot, to a coat which is more than half white. Many of these variations in amount of spotting are inherited and have been ascribed to the action of modifying factors which affect the amount of pigment produced. They may be present but not expressed in self-colored or albino mice and are inherited independently of the spotting factors, but they only express themselves *in the presence of factors for white spotting*. The best demonstration of this sort of factor interaction has been provided by experiments with *Drosophila*, where seven factors have been identified, each of which produces a qualitative effect on white eye color, which is itself due to a single factor. The effects of modifying factors may be cumulative, two factors giving a greater effect than one, as in the case of white spotting, or qualitative as in the case of eye colors in *Drosophila*. All factors probably partake of the nature of modifiers, since each factor appears to affect many characters and to alter the expression of other factors.

Multiple Effects of a Single Factor.—Not less important, perhaps, than the operation of many factors in producing a single character is the effect of a single factor upon many different characters. A number of instances of this manifold effect have recently come to light. A factor has frequently been spoken of as though it affected but a single trait in the individual, expressing itself in some more or less definite and limited way, suchas by a difference in eye color, or flower color, or the presence or absence of horns. Although it is convenient to name and refer to a factor by its most peculiar or striking manifestation, this custom should not conceal the fact that its most noticeable expression may not be its only one, nor even always its most important one.

A simple example of the widespread effect of a single factor may be seen in one of the traits which Mendel himself studied. He noted that the plants which bore purple flowers had also reddish spots in the axils of the leaves, and bore seeds with gray or brown seed coats. His evidence showed that this type differed by only one factor from the type which had white flowers, green stems and leaf axils, and white seed coats. It is easy to see that in this case the factor affected pigment development in general, and that the many differences between purple- and white-flowered plants were but local expressions of one fundamental difference. The same differences may be noted between the colored- and white-flowered varieties of many cultivated plants, such as the Jimson weed, the columbine, and others.

Of less obvious nature are the examples in which a single factor is known to affect different parts of the organism in a variety of apparently unrelated ways. Thus in the wild Jimson weed the large seed capsules are covered with sharp spines, whereas in one variety which has been bred under cultivation spines are lacking, and the capsules are smooth. This difference is conspicuous and behaves as a single unit in inheritance, the spiny type being dominant. These two types also differ, however, in many other characters, such as the length of the internodes, the stoutness of the stems, the angle of branching, the relative development of the short lateral branches, and other particulars. Here one factor evidently affects all sorts of traits all over the plant body.

Finally, in the fruit fly, *Drosophila*, it has been shown by Muller that a single factor is responsible for length and shape of the wings; presence or absence of elevations on the sides of the thorax, with characteristic disarrangement of the bristles called "vortices;" viability, which in extreme cases shows a lethal effect; infertility; and abnormally shaped abdomen.

All of the diverse effects of a single factor may not be shown under a constant set of conditions. One factor in *Drosophila*, known as "bent" from a peculiar effect which it has on the shape of the wings, is expressed under ordinary conditions in various changes in the wings and in a shortening and twisting of the legs; but when bent flies are reared in a cold atmosphere, a number of other peculiarities appear. The compound eyes become speckled and roughened because of irregularities in the hairs between the facets; one of the veins in the wing appears

broken, and the pattern of the bristle arrangement on the thorax is disturbed. The bent factor itself is not altered by the lower temperature, but many effects of this factor which are not apparent at ordinary temperatures are made visible by the cold.

These considerations serve to emphasize the conclusion already stated several times, that the real unit of inheritance is not the developed character which is visible and measurable, and which, as has been seen, may be variable and complex, but an invisible something in the germ cell called a factor or gene. Not only is the organism formed under the coöperative influence of a large number of these factors, but each factor, itself a distinct unit, exerts a widespread influence on many parts of the organism. The extreme extension of this view may be seen in the idea that many fundamental characters of the organism, such as size, are determined by factors acting on the whole animal or plant rather than on single parts.

Lethal Factors.—In all examples thus far cited consideration has been given to some of the ways whereby the factors which make up the genetic constitution of the organism actually express themselves in those characteristics which the organism displays, and it has been seen that certain factors may greatly modify the expression of others. There is still another series of factors, however, which produce such an extreme modification that at some point in its course they stop the development of the individual, and death ensues. Factors which have a fatal effect of this sort are known as *lethal* factors and are now recognized as of rather frequent occurrence among all sorts of animals and plants. They exhibit their peculiar effects, however, only when present in a *homozygous* condition. Lethal factors in the heterozygous condition may be carried with impunity by perfectly normal individuals, but that portion of the offspring of such individuals in which segregation has brought two lethals together will perish.

Albino Plants.—The complications introduced by the presence of lethal factors may be illustrated by a common occurrence in the breeding of corn and of sorghum. When the self-fertilized seeds from an apparently normal green plant are sown in the field, it sometimes happens that among the seedlings a number of spindling white plants are found which soon die because they lack chlorophyll, which is essential in the manufacture of food and hence in the life of the plant. When seeds from a plant which has pro-

duced such "albino" seedlings are carefully sown and the numbers of green and white seelings are counted, it is found that the green seedlings outnumber the white by about three to one (Fig. 43). The parent plant was apparently heterozygous for a factor for white (absence of chlorophyll) which is lethal when homozygous. Here the cause of the lethal effect produced by two white factors acting together is plain, since they prevent the development of a substance essential in the metabolism of the plant.

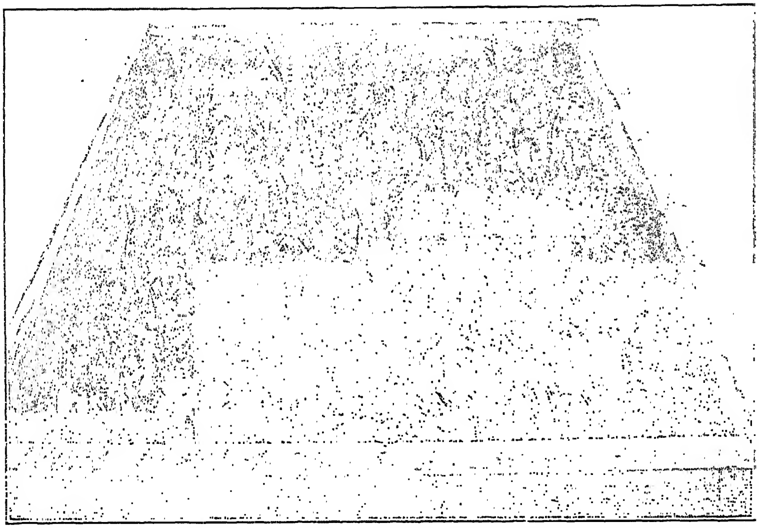


FIG. 43.—Seedlings from a cross of two green plants heterozygous for an albino lethal factor, showing segregation into three-fourths green and one-fourth albino plants. (*From Connor and Karper, in Journal of Heredity.*)

In Mice.—In most cases, however, the specific effect of the lethal cannot be ascertained, and it is known only that the ratios ordinarily expected from a given mating are altered by the death of a portion of the progeny. A notable case of this sort has been found among house mice. The yellow variety of this species, unlike all the others, resembles the Andalusian fowl, roan cattle, and similar types in the fact that it *never breeds true.* Matings between two yellows produce progeny of which about *two-thirds* are yellow like the parents, while *one-third* are of another color (black, brown, or gray). When yellows are bred to non-yellows, about half the young produced are yellow, while half are non-yellow. The latter ratio is that which is to

be expected from the mating of a heterozygote with a recessive, and suggests that yellow mice are heterozygous. When two such heterozygous yellows are mated, however, it would be expected that one-fourth would be pure yellow, one-half heterozygous yellow, and one-fourth non-yellow; but apparently *only the two latter classes* are born from such matings, and these occur in the proportion (as expected) of two yellow to one non-yellow. It has been found that all three classes of individuals are probably formed and begin their development, but that the

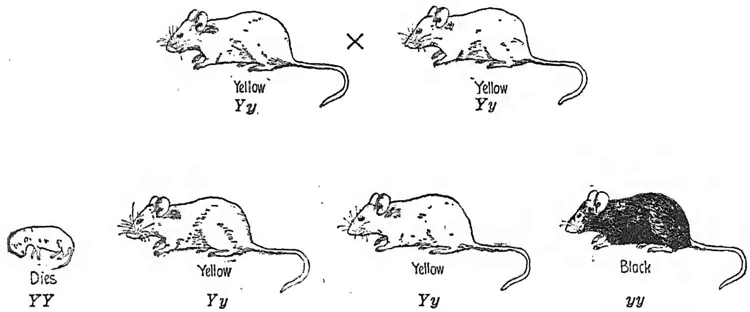


FIG. 44.—Inheritance of a lethal factor in mice. A mating of yellow by yellow giving one-fourth dead embryos, one-half yellow mice and one-fourth non-yellow ones.

pure yellows die while still within the body of the mother and only the heterozygous yellows and the non-yellows live to be born (Fig. 44). In conformity with this explanation the litters born from matings between yellows are smaller by about one-fourth than litters from yellow by non-yellow. This case may be represented by a diagram, as follows:

Y = a dominant factor for yellow
y = a recessive factor for non-yellow

Parents............	Yellow Yy	$\times$	Yellow Yy		
Gametes...........	Yy		$Y\ y$		
Progeny...........	YY	Yy	Yy		yy
	Pure yellow	Yellow	Yellow		non-yellow
	die	live			live
	25 per cent	50 per cent			25 per cent

In explanation of this case it is assumed that the union of two yellow factors produces an interaction which is fatal in some way to the developing embryo. A mouse which inherits a factor for

yellow can survive only if it receives also the allelomorphic factor for non-yellow. The expression of the character yellow depends, therefore, on the simultaneous presence of the factor for yellow and of its allelomorph.

A large number of factors which express themselves in this way are known in the plants and animals which have been most thoroughly studied, for example the corn plant and the fruit fly. In the latter about forty distinct lethal factors have thus far been distinguished. Not all of these cause death at the same stage of development. Some destroy the fertilized egg; others bring about the death of the newly hatched larva, occasionally through causes which can be specified, such as tumors; while others do not produce their lethal effect until the fly has reached the pupal or even the adult stage. The coming together of two lethal factors in a homozygous condition also probably accounts for a portion of the abnormally high rate of mortality which distinguishes some races of animals and plants.

In many of the cases reported, the lethal factor expresses itself in other ways, in addition to causing death. Thus in mice one lethal factor produces the yellow coat color and another influences spotting or the distribution of a white pattern in the coat; while in the fruit fly one lethal affects the shape of the wings, another the color of the eyes, and so on. That lethal factors are so often associated with characters of this sort and are operative only in a homozygous condition has been suggested as an explanation for the fact that so many "pure strains" of animals and plants, in which the individuals necessarily have many homozygous factors, are often so much less vigorous than the normal wild or mixed type. In the fruit fly, for example, the average life span of a wingless variety known as "vestigial" (Fig. 21) is only about half that of the wild race. This comparison has been made in the laboratory where both strains can be given identical conditions and where the possession of perfect wings is of no advantage. Both the vestigial-winged condition and the short duration of life are inherited, and apparently together, so that we may say that one effect of the vestigial factor in homozygous condition is to shorten the life of its possessor.

The relationship of such an important group of factors to the study of mortality is obvious. They have been mentioned here, however, principally because they illustrate a special type of factor expression which must be taken into account in a

successful interpretation of the results of many breeding experiments.

The Effect of the Environment on Factor Expression.—The characteristics which an organism displays are not only due to a complex of specific genetic factors with definite interactions, but depend to a very considerable extent upon the environment under which these factors find expression in the development of the individual. A rough distinction may be drawn between the external environment, those various agencies outside the body of the organism which may have an influence upon it, such as temperature, light, gravity, chemical substances, and so on; and the internal environment, including all those stimuli which have their origin within the body itself.

The External Environment.—In a previous chapter attention has been called to the profound effect which differences in the

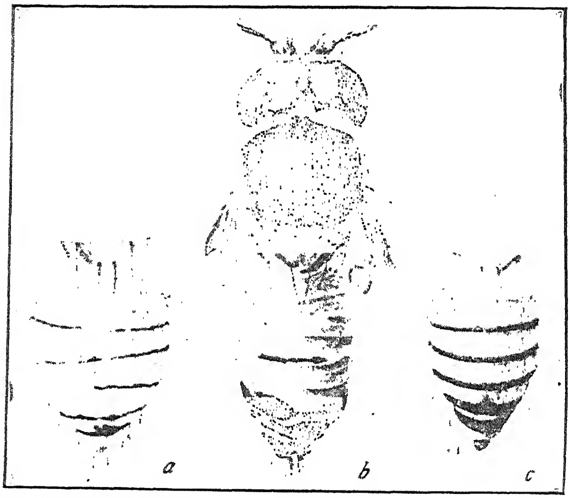


FIG. 45.—Abnormal abdomen in *Drosophila*, a mutant character the development of which is dependent on moisture. (*a*) abnormal female; (*b*) abnormal male; (*c*) normal female. (*From Morgan.*)

external environment produce on the visible characteristics of genetically similar individuals. Soil conditions, moisture, temperature, food, parasites, and similar agencies may in some cases so alter the expression of genetic factors as to mask or obscure their action entirely.

In the fruit fly, for example, the character "abnormal abdomen," in which the black bands on the abdomen are irregular or

absent entirely (Fig. 45), has been found to be due to a dominant mendelian factor, which expresses itself fully (i.e., produces the typical abnormal character) *only when the flies are reared on a moist culture medium.* When reared on dry food, flies possessing this factor have normal abdomens. Normal "many-noded" Jimson weeds in the same way differ from smaller "few-noded" ones by a single dominant factor, but in rich soil the few-noded plants grow so vigorously that they may resemble the normal type. Such variations as abnormal abdomen or few nodes thus result from an interaction between a genetic factor and a particular set of environmental conditions, and such cases warn one to use great care in ascribing a given effect either to the environment or to a genetic factor exclusively.

The Internal Environment.—In the higher animals, the various internal secretions, notably those which enter the blood from the ductless glands and which are called *hormones*, have a marked influence upon many physical and mental features. Some of these hormones regulate and correlate the general processes of development, and the attainment of normal maturity depends upon their presence in proper amount. Others regulate growth in particular tissues or regions, and abnormalities in the supply of these result in such conditions as goiter, abnormalities of the bones, and other specific defects. An interdependence exists between such internal agencies and genetic factors which is similar to the interaction between the environment and the inherited constitution.

A specific example of interaction between such hormones and a genetic factor has been found in the peculiar variation known as hen-feathering in certain breeds of fowls (Sebrights and Campines). In most varieties of fowls the male and female differ considerably in the form and distribution of the feathers (Fig. 68, page 199). In a few breeds however, there are strains in which the males have the female type of feathering. Members of such hen-feathered races apparently differ from those in which normal cock-feathering is the rule by a dominant factor for hen-feathering, which although it is expressed only in the males (females always being hen-feathered) is transmitted equally through both males and females. The factor for hen-feathering seems to depend for its expression on the internal secretion of the male sex glands. Morgan has found that when hen-feathered cocks are castrated, they assume typical male plumage (Fig. 46).

Two agencies then coöperate or interact to produce the character hen-feathering: (1) a genetic factor and (2) an internal secretion. When either is absent, the character does not appear.

Many other traits in animals are apparently dependent on the sex of the individual. These are not confined to the sexual organs themselves but extend to many others. The sexes in birds are generally distinguishable by differences in plumage, development of combs, wattles and spurs, voice, behavior, and other traits. In mammals the males often differ widely from the females by the presence of horns, as in some kinds of sheep and deer; in development of hair, as in the mane of the male lion,

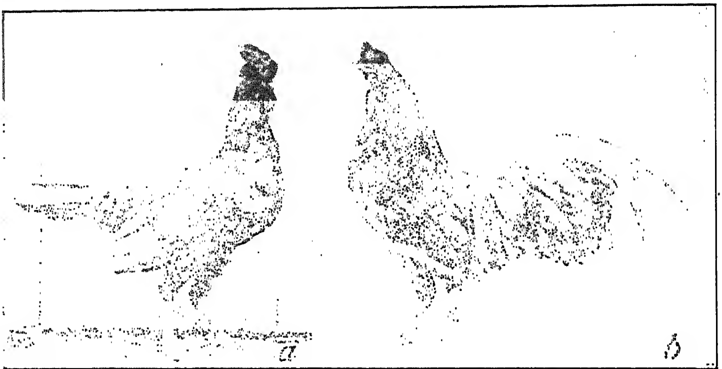


FIG. 46.—The effect of castration on type of plumage in poultry. At left (*a*) a hen-feathered Sebright cock. At right (*b*) a similar cock which was castrated and subsequently developed characteristic cock-feathering. (*From Morgan, courtesy Henry Holt and Co.*)

and in man by the growth of the beard and deeper voice, as well as in certain psychic characteristics. Many of these secondary sexual or *sex-limited* differences are inherited and are also directly traceable to the presence of the sexual glands themselves, since when these are removed by castration or affected by disease, the characters which normally accompany them disappear or fail to develop. The sexual glands apparently function also as ductless glands, and secrete hormones or similar substances into the blood which markedly affect the characters of the individual. Thus the expression of the inherited constitution of the individual may depend in a very important way on sex and other internal conditions.

Complexity of the Problem.—The examples used to illustrate the various types of factor expression and interaction are only a few

of the very many which investigation during the past twenty-five years has brought to light. Mendelism was hailed as a means of simplifying the problems of heredity, but as knowledge has increased it has been found to involve all sorts of unsuspected complications. These have often been so intricate and obscure as to suggest, at first, that they were unexplainable in simple terms, but advancing knowledge has brought them one by one into harmony with the underlying principles enunciated by Mendel. Since many of the puzzling cases of the past have been resolved by mendelian experiments, it is probable that the new and more difficult problems encountered in experimental breeding will, on careful analysis, yield to this method and be reconciled with already familiar principles. Far from being discouraging, these complexities should serve to point the way whereby the application of genetic theory may be extended further and further until all the manifold facts of inheritance may in time receive a full explanation.

QUESTIONS FOR THOUGHT AND DISCUSSION

48. How could you most easily distinguish the various genotypes among the walnut-combed F_2 birds in the checkerboard in Fig. 35?

49. Would you be able to establish a true-breeding race of walnut-combed fowls by selecting only walnut-combed birds for breeding? Can you suggest a more effective method for accomplishing this same result?

50. Do you think that the coat colors of rodents which have varied from the agouti pattern are of greater or less value to the animal than the wild pattern?

51. A strain of black, solid-colored mice has bred true for ten generations, except for one albino which appeared in the second generation. In the sixth generation a black- and white-spotted mouse is born in this strain. The breeder's explanation is that the blacks have been carrying white as a latent character and that, through long association, the two traits have affected or "contaminated" each other, resulting in a black and white animal. Criticize this explanation and offer an alternative one.

52. The difference between dark and blue eyes in man is probably determined by a single factor, but there are many shades of brown and of blue eyes. How would you explain these minor differences?

53. Can you suggest a chemical or physical explanation for the multiple effects of a single factor such as Mendel found in purple-flowered peas?

54. What cases in man can you suggest which seem to be instances of the multiple effects of a single factor?

55. In mice how would you recognize a recessive trait which has also a lethal effect?

56. When food and moisture are abundant, the character known as "abnormal abdomen" in *Drosophila* acts as a dominant over the normal type. Under dry conditions, all flies are normal, the abnormal abdomen failing to express itself whether the factor for it is present or not. Would you say that abnormal abdomen acts as a recessive under the second set of conditions? What similarities and differences are there, with regard to dominance and recessiveness, between the inheritance of this trait and that of horns in sheep (page 87)?

57. Describe one or more instances in man where the expression of an inherited defect has been modified by training or environment.

58. What do you think led to the origin and development of such secondary sexual characters as the brilliant plumage of male birds?

PROBLEMS

65. If a Dorset (horned) ram is bred to a Suffolk (hornless) ewe and the F_1 animals bred back to their parents, what will be the appearance of their offspring, as to horns?

Note.—In sheep, white fleece (W) is dominant over black (w); and the horned condition (H) is dominant over the hornless (h) in males but recessive in females.

66. If a homozygous horned, white ram is bred to a homozygous hornless, black ewe, what will be the appearance of the F_1 and the F_2 as to color and horns?

67. A horned, black ram bred to a hornless, white ewe has the following offspring: Of the males, one-fourth are horned, white; one-fourth horned, black; one-fourth hornless, white; and one-fourth hornless, black. Of the females, one-half are hornless, black and one-half hornless, white. What are the genotypes of the parents?

68. A horned, white ram is bred to the following four ewes and has one offspring by the first three, two by the fourth.

Ewe A is hornless and black. Her offspring is a horned, white female.

Ewe B is hornless and white. Her offspring is a hornless, black female.

Ewe C is horned and black. Her offspring is a horned, white female.

Ewe D is hornless and white. Her offspring are one hornless, black male and one horned, white female. What are the genotypes of these five parents as to color and horns?

69. A horned, black ram bred to a horned, white ewe produces a hornless, black female. If other females were to be raised from this mating, what proportion of them might be expected to resemble their mother in color and horns?

Note.—In man, assume that baldness (S) is dominant over non-baldness (s) in males but recessive in females.

70. A brown-eyed, bald man, whose father was non-bald and blue-eyed, marries a blue-eyed, non-bald woman whose father was bald and all of whose brothers were also bald. What will be the probable appearance of their children as to eye color and baldness?

71. A non-bald, brown-eyed, right-handed man marries a non-bald, brown-eyed, left-handed woman. They have three children: a bald, brown-eyed, right-handed son; a non-bald, blue-eyed, right-handed daughter; and a non-bald, brown-eyed, left-handed son. What are the genotypes of the parents?

Note.—In poultry the factors for rose comb (R) and pea comb (P), if present together, produce walnut comb. The recessive allelomorphs of both, when present together in a homozygous condition, produce single comb.

72. What will be the comb character of the offspring of the following crosses, in which the genotypes of the parents are given?

$Rr\ Pp \times Rr\ Pp$	$Rr\ Pp \times Rr\ pp$
$RR\ Pp \times rr\ Pp$	$Rr\ pp \times rr\ Pp$
$rr\ PP \times Rr\ Pp$	$Rr\ pp \times Rr\ pp$

Note.—In the following five questions, all of which concern comb form in poultry, determine the genotypes of the parents:

73. A rose crossed with a walnut produces offspring three-eighths of which are walnut, three-eighths rose, one-eighth pea, and one-eighth single.

74. A walnut crossed with a single produces offspring one-fourth of which are walnut, one-fourth rose, one-fourth pea, and one-fourth single.

75. A rose crossed with a pea produces six walnut and five rose offspring.

76. A walnut crossed with a single produces one single-comb offspring.

77. A walnut crossed with a walnut produces one rose, two walnut, and one single offspring.

78. If one of the walnut parents in the preceding question were crossed with one of its single-comb offspring, what would *their* offspring be like?

Note.—In poultry, feathered shanks (F) are dominant over clean (f); and the white plumage of Leghorns (I) is dominant over black (i).

79. What will be the appearance of the offspring of the following crosses, in which the genotypes of the parents are given:

$$ff\,Rr\,Pp \times Ff\,Rr\,pp$$
$$Ff\,ii\,Rr\,pp \times ff\,II\,Rr\,Pp$$

80. A feathered-shanked, rose-comb bird crossed with a clean-shanked, pea-comb one produces 25 feathered, pea offspring; 24 feathered, walnut; 26 feathered, rose; and 22 feathered, single. What are the genotypes of the parents?

81. A feathered-shanked, white, rose-comb bird crossed with a clean-shanked, white, walnut-comb one produces the following offspring: two feathered, white, rose; four clean, white, walnut; three feathered, black, pea; one clean, black, single; one feathered, white, single; two clean, white, rose. What are the genotypes of the parents?

82. A feathered-shanked, white, walnut-comb bird crossed with a clean-shanked, white, pea-comb one produces a single offspring, which is clean-shanked, black, and single-comb. In further offspring from this cross, what proportion may be expected to resemble each parent, respectively?

83. A breeder has a homozygous race of feather-legged, black, rose-comb birds and another of clean-legged, white, pea-comb ones. He wants a race of black birds which have clean legs and walnut combs. What proportion of the F_2 raised from a cross between these two races will be what he desires in *appearance?* What proportion of these birds will be homozygous for the desired characters?

84. Assume that white and black plumage color in the following case behaves as in Andalusian fowls. Cross a homozygous feathered-shanked, white, rose-comb bird with a homozygous, clean-shanked, black, pea-comb one. What will be the appearance of the F_1? In the F_2, what proportion of the birds will resemble, in the appearance of all the characters, the black parent? the white parent? the F_1?

Note.—In sweet peas, factors C or P alone produce white flowers, the purple color being due to the presence of both these factors in the genotype.

85. What will be the flower color of the offspring of the following crosses, in which the genotypes of the parents are given?

$Cc\,Pp \times cc\,Pp$	$cc\,Pp \times CC\,pp$
$Cc\,Pp \times Cc\,PP$	$Cc\,pp \times cc\,Pp$

86. In the checkerboard (Fig. 36) what will be the flower color of the offspring of each of the nine purple-flowered plants if selfed?

Note.—In the following three crosses of sweet peas, what are the genotypes of the parents?

87. A white-flowered plant crossed with a purple produces offspring of which three-eighths are purple and five-eighths white.

88. A purple-flowered plant crossed with a white one produces offspring of which one-half are purple and one-half white.

89. A white-flowered plant crossed with another white produces offspring of which three-fourths are white and one-fourth purple.

90. Cross one of the purple-flowered offspring in the last question back on each of its parents. What will be the appearance of the offspring in each case?

Note.—In corn, factors C and R are both necessary for the production of red aleurone color, the absence of either resulting in white aleurone. If factor P is present in addition to C and R, the aleurone is purple, but P has no effect in the absence of either C or R or both.

91. In corn, what is the aleurone color of the offspring of the following crosses, the genotypes of the parents being given?

$Cc\ Rr\ pp \times cc\ Rr\ Pp$	$CC\ rr\ Pp \times Cc\ Rr\ pp$
$cc\ RR\ Pp \times Cc\ Rr\ pp$	$Cc\ Rr\ Pp \times Cc\ Rr\ Pp$

Note.—In the following three questions, all of which refer to aleurone color in corn, find the genotypes of the parents.

92. A purple plant crossed with a white produces offspring of which one-eighth are purple, one-eighth red, and three-fourths white.

93. A purple plant crossed with a red produces offspring of which nine thirty-seconds are purple, nine thirty-seconds red, and seven-sixteenths white.

94. A purple plant crossed with a white produces offspring of which three-eighths are purple and five-eighths white.

Note.—In corn, factor W prevents the appearance of any color in the aleurone at all, and its presence thus results in white aleurone. Its recessive allelomorph w allows the development of color.

95. What will be the aleurone color of the offspring of the following crosses, the genotypes of the parents being given?

$Ww\ Cc\ Rr\ Pp \times ww\ cc\ rr\ pp$	$ww\ Cc\ rr\ Pp \times WW\ cc\ rr\ Pp$
$Ww\ cc\ Rr\ pp \times Ww\ cc\ Rr\ pp$	$ww\ cc\ Rr\ pp \times Ww\ Cc\ rr\ PP$

Note.—The effect of the factors C, A, B, D, P, and S, and their recessive allelomorphs on coat color in mice, are as follows (See Table V)

C, colored	aB, black
c, albino	ab, brown
AB, agouti	D, normal dark color
Ab, cinnamon	d, dilute color

P, normal dark eyes
p, pink eyes

S, solid or self color
s, spotted with white

96. In mice, what will be the coat color of the offspring of the following crosses, in which the genotypes of the parents are given?

$$Cc\ Aa\ Bb \times CC\ aa\ Bb$$
$$Cc\ Aa\ bb \times cc\ aa\ Bb$$
$$Cc\ Aa\ BB\ Dd \times cc\ Aa\ Bb\ Dd$$
$$CC\ aa\ Bb\ dd\ Pp \times Cc\ aa\ Bb\ Dd\ pp$$
$$CC\ AA\ BB\ Dd\ Pp\ SS \times Cc\ aa\ Bb\ DD\ Pp\ ss$$
$$cc\ Aa\ bb\ Dd\ pp\ Ss \times Cc\ aa\ Bb\ dd\ Pp\ ss$$
$$CC\ aa\ Bb\ Dd\ Pp\ ss \times cc\ Aa\ bb\ dd\ pp\ Ss$$
$$Cc\ aa\ BB\ DD\ pp\ ss \times CC\ aa\ BB\ dd\ PP\ SS$$

Note.—In the following six crosses, which deal with coat color in mice, find the genotypes of the parents.

97. An agouti animal crossed with another agouti produces offspring of which nine-sixteenths are agouti, three-sixteenths black, three-sixteenths cinnamon, and one-sixteenth brown.

98. A cinnamon animal crossed with an albino produces offspring of which three-eighths are agouti, one-eighth black, and one-half albino.

99. A black animal crossed with an agouti produces offspring of which nine thirty-seconds are agouti, nine thirty-seconds black, three thirty-seconds cinnamon, three thirty-seconds brown, and one-fourth albino.

100. A dilute cinnamon animal crossed with an albino produces three agouti offspring, three dilute agouti, one spotted agouti, and one dilute, spotted agouti.

101. A dilute agouti animal crossed with a pink-eyed, spotted black produces three agouti offspring, one spotted agouti, two dilute agouti, two dilute, spotted agouti, four cinnamon, one spotted cinnamon, two dilute cinnamon, and four albinos.

102. An agouti animal crossed with a dilute pink-eyed, spotted brown produces one dilute black, one spotted agouti, and one pink-eyed cinnamon.

103. A breeder has a race of dilute, pink-eyed spotted brown mice and also has some wild stock (homozygous agouti). He wants to transfer the pink-eyed character to the agouti race and get a pure race of pink-eyed agouti animals. If he crosses his two races, how large an F_2 should he raise to get the desired type? If he has more time, how can he obtain the same result without raising so many animals? How can he tell when he gets the homozygous type which he wishes?

Note.—In summer squashes the factor for white fruit color (W) is epistatic to that for yellow (Y); WY and Wy plants are white, wY plants yellow, and wy plants green.

104. What is the color of the fruit in the offspring of the following crosses, the genotypes of the parents being given?

$Ww\ Yy \times Ww\ yy$ $\quad$ $ww\ YY \times Ww\ yy$ $\quad$ $Ww\ yy \times ww\ Yy$

Note.—In the following three questions, which deal with fruit color in squashes, find the genotypes of the parents.

105. A white plant crossed with a yellow one produces offspring of which one-half are white, three-eighths yellow, and one-eighth green.

106. A white plant crossed with a green one produces offspring of which one-half are white and one-half yellow.

107. A white plant crossed with another white one produces offspring of which three-fourths are white, three-sixteenths yellow, and one-sixteenth green.

Note.—In summer squashes, disc fruit shape, D, is dominant over sphere fruit shape, d.

108. What is the appearance of the offspring of the following squash crosses as to shape and color of fruit?

$Dd\ Ww\ yy \times dd\ Ww\ YY$ $\quad$ $dd\ Ww\ Yy \times Dd\ ww\ Yy$

$DD\ ww\ Yy \times Dd\ Ww\ Yy$ $\quad$ $Dd\ ww\ Yy \times dd\ WW\ Yy$

$dd\ Ww\ yy \times dd\ ww\ Yy$ $\quad$ $Dd\ ww\ Yy \times Dd\ Ww\ Yy$

Note.—In the following three questions, which deal with shape and color of fruit in squashes, determine the genotypes of the parents:

109. A white disc plant crossed with a green disc one produces offspring of which three-eighths are white disc, three-eighths yellow disc, one-eighth white sphere, and one-eighth yellow sphere.

110. A white disc plant crossed with a yellow disc one produces offspring of which three-eighths are white disc, one-eighth white sphere, nine thirty-seconds yellow disc, three thirty-seconds yellow sphere, three thirty-seconds green disc, and one thirty-second green sphere.

111. A white sphere plant crossed with a white disc one produces seven white disc plants, six white sphere, two yellow disc, one green sphere, and one green disc.

Note.—In stocks, factor C, in the absence of factor R, produces cream-colored flowers; c produces white ones; C with R, red ones; C with R and V, violet ones, but V has no effect in the absence of either C or R or both. Factor H causes the plant to be hairy, but it is operative *only in the presence of both* C *and* R. Its recessive allelomorph, h, causes a smooth condition. White-flowered and cream-flowered plants are thus always smooth, and red-flowered and violet-flowered ones may be either hairy or smooth.

112. In stocks, what is the appearance of the offspring of the following crosses, the genotypes of the parents for flower color and plant surface being given?

$CC\ Rr\ VV\ Hh \times Cc\ rr\ Vv\ HH$ $\qquad$ $Cc\ rr\ vv\ Hh \times cc\ RR\ Vv\ hh$

$Cc\ Rr\ Vv\ Hh \times Cc\ Rr\ Vv\ Hh$ $\qquad$ $Cc\ Rr\ Vv\ Hh \times cc\ rr\ vv\ hh$

Note.—In the following three questions, which deal with flower color and plant surface in stocks, find the genotypes of the parents:

113. A cream, smooth plant crossed with a white smooth one produces offspring of which three-eighths are violet smooth, one-eighth red, smooth, and one-half white smooth.

114. A violet smooth plant crossed with a white smooth one produces offspring of which one-sixteenth are violet hairy, one-sixteenth violet smooth, one-sixteenth red hairy, one-sixteenth red smooth, one-fourth cream smooth, and one-half white smooth.

115. A violet, hairy plant crossed with a red, smooth one produces one white, smooth plant, one cream, smooth one, and one red, smooth one. What are the chances of getting a violet hairy plant out of this cross?

Note.—In Four-o'clocks there are two factors, Y and R, which affect flower color. Neither is completely dominant, and the two interact on each other to produce seven different flower colors, as follows:

$YY\ RR$ = crimson $\qquad$ $Yy\ RR$ = magenta

$YY\ Rr$ = orange-red $\qquad$ $Yy\ Rr$ = magenta-rose

$YY\ rr$ = yellow $\qquad$ $Yy\ rr$ = pale yellow

$yy\ RR$ and $yy\ rr$ = white

116. In Four-o'clocks, cross a crimson-flowered plant with a white one ($yy\ rr$). What will be the appearance of the F_1? of the F_2? of the offspring of the F_1 crossed back on its crimson parent? on its white parent?

117. What will be the flower color in the offspring of the following Four-o'clock crosses?

$YY\ Rr \times yy\ Rr$ $\qquad$ $Yy\ rr \times yy\ Rr$

118. Two Four-o'clock plants (color unknown) give the following offspring when crossed: one-eighth crimson, one-eighth orange-red, one-fourth magenta, one-fourth magenta-rose, and one-fourth white. What were the genotypes of the parents?

Note.—In poultry I is a dominant factor for white plumage. Its recessive allelomorph, i, allows the development of color. Factor C produces colored plumage (in the absence of I), and c causes the appearance of recessive white plumage.

119. What will be the plumage color of the offspring of the following crosses in poultry, the genotypes of the parents being given?

Ii Cc × *ii Cc*	*ii Cc* × *Ii CC*
II cc × *ii cc*	*Ii cc* × *ii Cc*

120. From the data on inheritance of capsule shape in the shepherd's purse calculate the expected results in F_2 from self-fertilizing each of the fifteen F_2 types with triangular capsules in Fig. 41.

121. In the checkerboard showing inheritance of two factors for grain color in wheat (Fig. 42), what results should be obtained by selfing the F_2 red-grained plants? By selfing the F_2 white-grained plants?

122. Two strains of corn have been found in each of which plants occur which, when selfed, produce about three-fourths normal green and one-fourth lethal white ("albino") seedlings. If two such albino-producing plants, one from each strain, are crossed, the F_1 is found to be all green, but certain of the F_2 populations are approximately nine-sixteenths green and seven-sixteenths white. Explain, giving genotypes.

123. In corn, plant *A* when crossed with plant *B* produced 255 green and 89 white offspring, but when selfed produced 153 green and 118 white offspring. What are the genotypes of these two plants? What should plant *B* produce when selfed? (Data adapted from Demerec.)

124. A green corn plant when selfed produces about fifteen-sixteenths green and one-sixteenth white (lethal) seedlings. Explain.

125. In mice the waltzing habit is recessive to normal gait. A yellow self-colored (*SS*) male carrying black is mated with a black-spotted waltzing female. What would be the result of back-crossing a yellow F_1 male to its mother?

126. If a bird from a hen-feathered race is crossed with one from a cock-feathered race, what will be the appearance of the F_1? of the F_2? of the F_1 crossed back on each parent?

REFERENCE ASSIGNMENTS

30. Describe a case of reversion in wild or domesticated animals or plants, and give the probable explanation of it.

31. Darwin observed that when domesticated breeds of pigeons are crossed, reversion frequently occurs to the color of the rock pigeon, *Columba livia*. What conclusion did he draw from this and what other evidence was necessary to prove his point?

32. Give an example, other than those cited in the text, of the multiple effects of a single factor.

33. Describe the inheritance of a lethal factor in *Drosophila*.

34. In grafting parts of two plants together, what effect does the plant used as the stock have on the characters developed by the scion?

35. What are the endocrine glands in man and what functions have been attributed to each?

36. Describe the inheritance of the various types of coat color in rabbits; in guinea pigs.

37. Give the derivation of the following terms and state in what way each is appropriate:

Hypostatic	Lethal
Epistatic	Hormone

CHAPTER VI

THE PHYSICAL BASIS OF INHERITANCE

The evidence for the theories of inheritance which have been discussed in the last few chapters has been derived almost wholly from breeding experiments with animals and plants. From the hereditary behavior of certain characters of adult or developed organisms a few fundamental laws have been inferred, which rest chiefly on the assumption that such characters are caused or influenced by specific and discrete units which are transmitted through the gametes. An understanding of the nature of factors and of inheritance in general must remain inferential and indirect until it is possible to find physical reasons for the observed facts of inheritance. An attempt will therefore be made in the next few chapters to correlate what is known of inheritance with other knowledge of the physical structure and functioning of organisms, particularly with respect to the reproductive process.

Inheritance, like growth, reproduction, and other fundamental activities of the organism, is an expression of the peculiar properties and organization of protoplasm. In multicellular animals and plants it is particularly an expression of the constitution of the protoplasm in the gametes. These cells, from which the mature plant or animal develops, do not differ essentially from the other cells of the body. A typical gamete consists of a nucleus and of cytoplasm which may be differentiated into various structures for the maintenance, protection, or locomotion of the cell. Within this apparently simple protoplasmic system must be contained all of the factors determining the inherited characters of the organism. These factors are found to be both specific and general in their effects and have the power of self-perpetuation which is common to all protoplasm. It is then from protoplasm that the first information on the physical basis of inheritance must be obtained, and particularly from protoplasm as it appears in the germ cells and in reproduction.

The Sexual Process in Animals.—Reproduction consists essentially in the production of a new individual by one or by

two older individuals. This is brought about in a variety of ways, as explained above (page 2). In all of the higher animals reproduction takes place by a sexual process, of which the essential feature is the union of two different and specialized sexual cells, the *gametes*, one of which is contributed by each of the two parents. The male parent produces male gametes (sperm or spermatozoa (Fig. 47)); the female parent produces female gametes (ova or eggs (Fig. 47)); and the union of these two cells to form the new individual is known as *fertilization*.

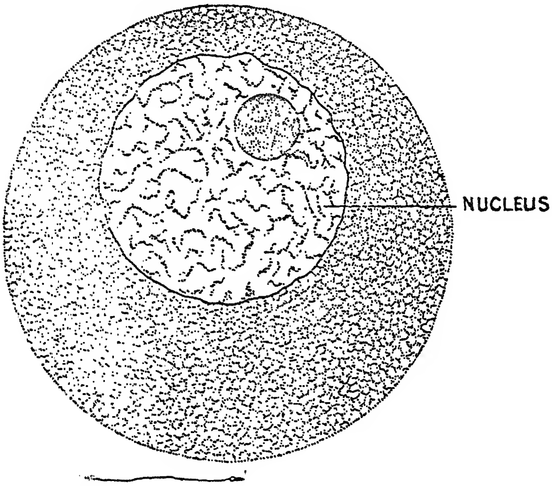


FIG. 47.—Egg (above) and sperm (below) of the sea urchin (× 750).[1]

The male gametes or spermatozoa are produced in the male sexual glands or testes by a peculiar process involving the multiplication and growth of the cells of the testes and their preparation for independent existence. This process is known as *spermatogenesis*, and as a result of it spermatozoa are produced in enormous numbers. Thousands of these microscopic gametes, in such animals as the fowl, the horse, and man, may be contained in a single drop of fluid. The length of the human spermatozoön has been estimated at about $\frac{1}{300}$ inch. Under the higher powers of the microscope these cells appear to have a form which is characteristic for a given species, but the sperm of all species agree in general features. They consist principally of a mass of densely staining material, chromatin, which forms

[1] From *The Cell in Development and Inheritance* by E. B. Wilson. Second edition, copyright 1900 by The Macmillan Company. Reprinted by permission.

the nucleus of the sperm cell. The spermatozoön is, in fact, little beside a cell nucleus with secondary structures which serve for protection and locomotion. In the higher animals these structures are always motile, and propel themselves by swimming in the thick fluid in which they are liberated from the testes. They are capable of independent existence sometimes for long periods. The sperm of the honey bee, for instance, may live for more than a year within the body of the female.

The female gametes or eggs are produced in the female sexual gland or ovary by a process known as *oögenesis* which, as in the male, serves to prepare the egg cell for its peculiar functions in reproduction. The egg (Fig. 47) like the sperm contains a single nucleus, but associated with this is usually a large mass of cytoplasm rich in stored food for the embryo, so that the egg is generally much larger than the sperm. The increase in size due to stored food reaches an extreme in some birds' eggs, which with the exception of a single microscopic nucleus consist entirely of inert food material (yolk and albumen) and the envelopes (shell and membranes) which are necessary for the protection of the contents and of the future embryo.

Fertilization.—The union of these two cells, egg and sperm, is, in the higher animals, brought about at the time of mating or copulation through the introduction by the male of fluid containing spermatozoa into the genital tract of the female. The spermatozoa move by their own efforts to the region of the ovary and one or more spermatozoa enter an egg. Eventually, one sperm nucleus fuses with the nucleus of the egg and the fertilized egg or *zygote* results. After fertilization the fused nucleus divides and the process of development of the embryo ensues.

The Sexual Process in Plants.—The sexual process in plants is somewhat complicated by the peculiarity of their life cycle known as the Alternation of Generations, a sexual plant giving rise to a non-sexual one which, in turn, produces a sexual plant again. This condition arose far back in the history of the plant kingdom and is seen in a simple form today in the ferns and their allies. Here the sexual plant or *gametophyte*, a small and inconspicuous structure, bears male sex organs or *antheridia* and female sex organs or *archegonia* which produce, respectively, male gametes, or sperms, and female gametes, or eggs. In the higher types of this group the two sexes are on separate plants, some of the gametophytes being male and some female. The fertilized egg develops not into another gametophyte but into a plant of

wholly different appearance and structure, a sexless *sporophyte*, the "plant" itself, with well-developed roots, stems, and leaves, the reproductive organs of which are known as *sporangia* and bear non-sexual reproductive cells, the *spores*. These germinate without any sexual process and each grows directly into a gametophyte. The spores are often of two kinds, smaller *microspores* and larger *megaspores*, which produce male and female gametophytes, respectively.

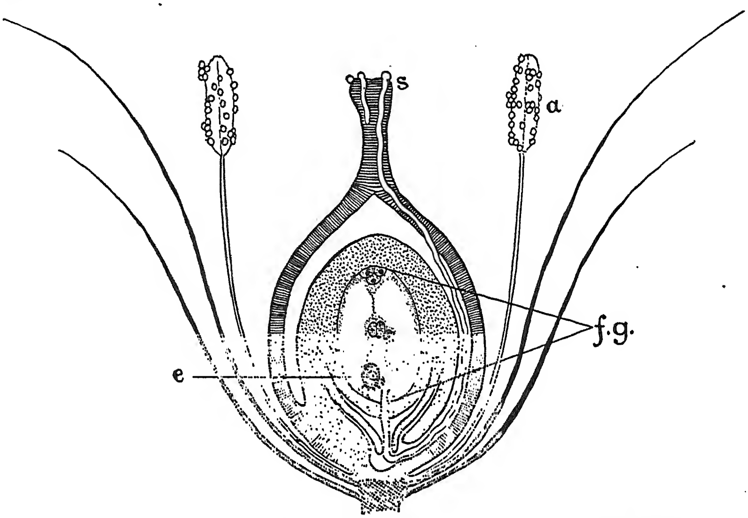


Fig. 48.—Diagram of a vertical section through a flower, showing pollination and fertilization. The anthers, *a*, have opened, liberating pollen grains, two of which have germinated on the stigma, *s*. The pollen tube from one of these has grown down the style and carried the two male gametes to the embryo sac or female gametophyte, *f. g.* of the ovule, where one is fertilizing the female gamete or egg, *e*. From the union of their nuclei will develop the embryo of the seed, which grows into a new plant.

Among the seed plants, with which genetics has been chiefly concerned, the gametophytic generation has become very greatly reduced and is no longer an independent plant but is contained wholly within the reproductive structures of the sporophyte, which is the "plant" which we see. These reproductive structures are commonly known as *flowers* (Fig. 48). Each consists, typically, of four sets of structures. Outside is a circle of protective parts, the *calyx*, and within this another circle of conspicuous and attractive parts, the *corolla*. Next occurs a series of "male" sexual organs, the *stamens*, each bearing an *anther*, which produces within itself a mass of single-celled *pollen*

grains. Strictly speaking, however, the anther is not a sexual organ but is a sporangium and the pollen grains are really microspores and not gametes, although they give rise directly to gametes. In the center of the flower is the "female" organ, the *pistil*, consisting of an *ovary*, *style*, and *stigma*. Within the ovary are one or more *ovules* which, after fertilization, develop into seeds. The ovule is really a sporangium, also, and produces within itself a megaspore which germinates into a very much reduced female gametophyte or *embryo sac*, containing at least one egg cell, the true female gamete. The pollen grain (microspore) is carried by wind, insects, or other agencies to the stigma of the same flower or another of the same species, and there germinates, its contents dividing into a small group of cells (in the higher plants only three) which represent the last vestige of the male gametophyte. From the germinating grain develops a *pollen tube* which penetrates the style and enters the ovule in the ovary. Down this tube passes the contents of the pollen grain, one non-sexual nucleus and two other nuclei, the true male gametes. One of these gametes unites with the egg cell in the ovule and from this fertilized egg develops the embryo of the seed. The second male nucleus unites with the endosperm nucleus and gives rise to the endosperm tissue of the seed.

The process by which the new individual is formed in both animals and plants consists in brief in the preparation of a single cell by each parent and in the union of the nuclei of these cells in the zygote. Reproduction is thus seen to be essentially a cellular process and a better understanding of its significance in inheritance will require a more detailed knowledge of the characteristics and behavior of cells.

The Structure of the Cell.[1]—The bodies of all plants and animals consist of minute units of protoplasm known as *cells*, a typical example of which is shown diagrammatically in Fig. 49. Although the size, shape, structure, and contents of cells vary with their functions and their location, there are a

[1] The study of cells is the province of a specialized branch of biology known as *cytology*. Since it has become increasingly evident that the explanation of the facts of inheritance must be sought in the structure and behavior of cells and of their parts, a knowledge of cytology has come to be more and more essential for the student of genetics. It is possible here to give only a short sketch of this important subject, but the interested student is directed for further information to the works of Sharp (1921) and of Wilson (1925) as listed in the bibliography.

number of features which are common to all of them. A cell may be defined as a *nucleus* or dense central mass of protoplasm surrounded by semifluid or less dense *cytoplasm*. Within each of these regions of the living cell, careful microscopic study has discovered a number of minute but definite structures. In the cytoplasm are found denser bodies, the chondriosomes, plastids, centrioles, and many kinds of granules. In the nucleus occurs a fine network of apparently fibrous material on which is supported a dense, usually granular mass, which from its affinity for

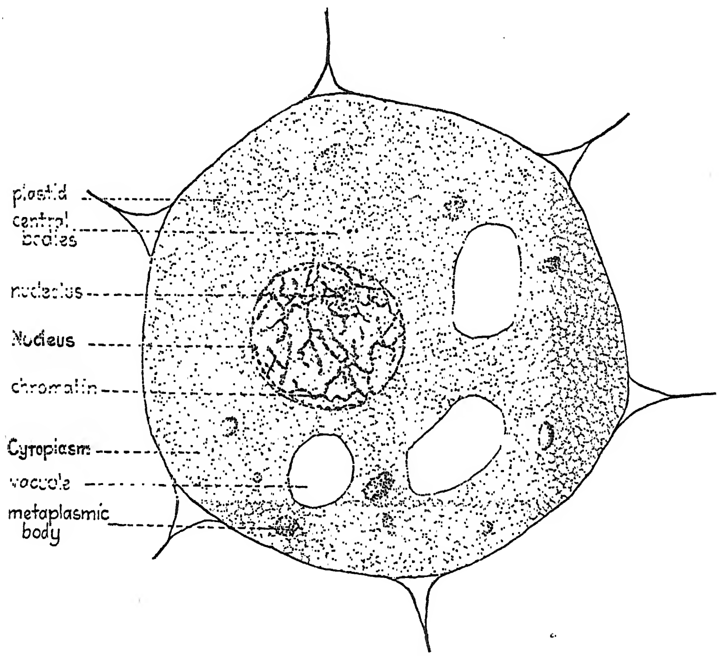


FIG. 49.—Diagrammatic drawing of a typical cell.

stains is known as *chromatin*. The functions of all of these structures within the cell are not certainly known. The bodies in the cytoplasm are apparently concerned with chemical transformations which are necessary for the nutrition and growth of protoplasm. This is certainly so for the plastids in the cytoplasm of plant cells, which are known to be involved in the synthesis of food and the production of other important substances. The nucleus, on the other hand, is thought to exercise a determining influence on the physiological activity, growth, and reproduction

of the cell, and to be of particular importance in heredity. All of the functions of the parts of the cell are closely correlated, for the whole cell functions as a unit. Each cell may be regarded as a complete organism, since it may often exist, grow, and reproduce by itself; and from a single cell may arise a complete and complex animal or plant.

It is not strange, therefore, that, as soon as modern biologists began to observe the facts of heredity, their attention should inevitably be turned toward the single cell which in sexual organisms forms the only bridge between parent and offspring. More particularly their attention was focused on the most constant and, in its behavior, the most remarkable feature of the cell, the nucleus. Even before the method of inheritance became known, the German biologist Weismann had suggested that this dominant structure of the cell was the seat of the hereditary material, and on this inference founded a consistent theory of inheritance. It was known, for instance, that in most cases the offspring inherit equally from the father and the mother; and that the only contribution of the father to the offspring is a single cell, the sperm, which consists almost entirely of nucleus. After the method of inheritance was discovered, the suspicion that the nucleus was chiefly involved in inheritance was greatly increased, for the exactness of the method by which the factors were found to be distributed to the germ cells demanded a physical mechanism of the same orderliness and exactitude. Just such a mechanism was apparent in the remarkable behavior of the nucleus, and a study of this behavior is, then, an important step in our search for the physical basis of inheritance.

The Nucleus in Cell Division.—Microscopic examination of properly prepared and stained tissues of animals and plants reveals that most of the cells are in an apparently quiescent or resting stage. The nucleus of such a resting cell is shown in Fig. 49. Very little detailed structure can be seen in such a nucleus. Wherever actively growing tissue is examined, however, many of the cells will be found to be undergoing multiplication. The prevailing mode of division is a complex and exact one and is known as *mitosis*.[1] This is the method by which the

[1] The nucleus and the cytoplasm may in rare cases simply divide without a complex mitotic process into two approximately equal parts, each of which becomes a new cell. This method of division, which is chiefly characteristic of senescent tissues, is known as *amitosis* or direct cell division.

[illegible] cells, in common with almost all others, are formed, and is particularly [illegible] for students of genetics, since it is chiefly at the time of mitotic division that the finer structure of the nucleus becomes visible.

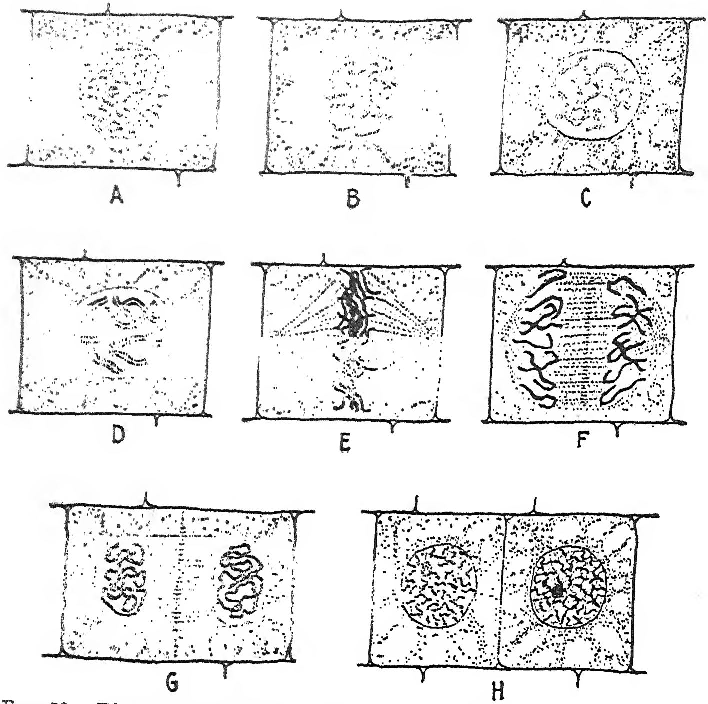


FIG. 50.—Diagram of cell division by mitosis. *A*, resting cell, the chromatin of the nucleus in a fine network. *B*, the chromatin is gathered into a long thread. *C*, this thread breaks up into chromosomes. *D*, each chromosome splits into two lengthwise. (*B*, *C*, and *D* are called *prophases*). *E*, *metaphase*. The split chromosomes arrange themselves in a plane across the equator of the cell, and the spindle, with its two poles, is formed. *F*, *anaphase*. The chromosome halves separate, one complete set (eight in this case) going to one pole and the other set to the other pole. *G*, *telophase*. Each new group of chromosomes arranges itself into a thread and a new cell wall begins to appear between the groups. *H*, two complete new cells, each with a nuclear content equal and similar to that of *A*.

The *process of mitosis* is described in Fig. 50 *A* to *H* and in the accompanying legend. This may seem a roundabout and complicated process for accomplishing what appears to be the simple object of dividing one nucleus into two equal halves. Thus instead of simple fission of the nucleus, the chromatin is seen to

go through a remarkable series of changes in which it first organizes itself into a long coiled thread, which later breaks into smaller pieces each of which divides lengthwise into two equal halves. These then condense into shorter rod-like structures, *the chromosomes* which still remain paired until one member of each pair is drawn to each of the two opposite poles. The result is the equal division of every part of the chromatin between each of the two daughter cells. The exactitude with which this is accomplished would seem to indicate that the chromatin is of especial importance, that particles of it are not all alike, and that it is necessary that the two daughter cells receive their share of each bit.

Individuality of the Chromosomes.—Detailed study under the higher powers of the microscope has further emphasized

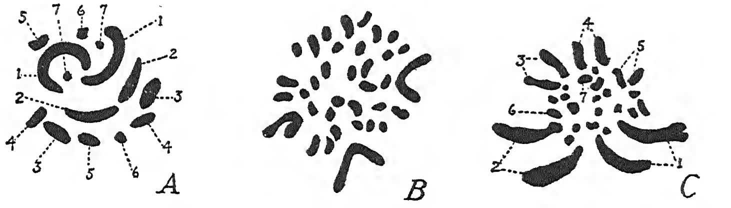


FIG. 51.—Individuality of the chromosomes. Chromosomes of a plant louse (*A*), beetle (*B*) and seed plant (*C*), showing similarities between the members of the same pair of chromosomes and differences between the pairs.[1]

this conclusion. In the first place, it is found not only that each species of animal or plant has a constant and typical number of chromosomes (Table VI), but that each chromosome probably differs in shape, size, and other particulars from every other one (Fig. 51). Each chromosome is, in fact, probably a specific organization of chromatin, with an individuality of its own. In the second place each thread-like chromosome is found to consist of a large number of small bead-like parts or units, the *chromomeres,* which are likewise probably individual in character and divide each into two equal halves when the nucleus divides. Further than this the evidence from the microscope has not gone and apparently cannot go, but with other evidence to be discussed later it is sufficient to indicate that the equality in the division of chromatin probably extends to the smallest particles

[1] From *The Cell in Development and Heredity* by E. B. Wilson. Third edition, copyright 1925 by the Macmillan Company. Reprinted by permission.

Table VI.—Examples of Chromosome Numbers in Animals and Plants
(*After Wilson*)

Species	Group	Haploid	Diploid
Animals			
Hydra	*Coelenterata*	6	12
Campanularia	*Coelenterata*	10	20
Ascaris (thread worm)	*Nemathelminthes*	1 and 2	2 and 4
Paragordius	*Nemathelminthes*	7	14
Lineus	*Nemertinea*	8	16
Cerebratulus	*Nemertinea*	16	32
Lumbricus (earth worm)	*Annelida*	16	32
Nephelis (leech)	*Annelida*	8	16
Helix (snail)	*Mollusca*	12 and 24	24 and 48
Crepidula (limpet)	*Mollusca*	30	60
Cyclops (water flea)	*Crustacea*	2	4
Cambarus (crayfish)	*Crustacea*	100	200
Periplaneta (cockroach)	*Insecta*	17	34
Pieris (cabbage butterfly)	*Insecta*	15	30
Lymantria (gypsy moth)	*Insecta*	31	62
Anopheles (mosquito)	*Insecta*	3	6
Drosophila (fruit fly)	*Insecta*	4	8
Musca (house fly)	*Insecta*	6	12
Salamandra	*Vertebrata*	12	24
Rana (frog)	*Vertebrata*	13	26
Columba (pigeon)	*Vertebrata*	8	16
Didelphys (oppossum)	*Vertebrata*	11	22*
(hedgehog)	*Vertebrata*	24	48*
(armadillo)	*Vertebrata*	30	60*
Lepus (rabbit)	*Vertebrata*	22	48*
Equus (horse)	*Vertebrata*	30	60*
Macacus (monkey)	*Vertebrata*	24	48*
Homo (man)	*Vertebrata*	24	48*
Plants			
Spirogyra	*Thallophyta*	12	24
Chlamydomonas	*Thallophyta*	30	60
Fucus (rockweed)	*Thallophyta*	32	64
Pyronema	*Thallophyta*	12	24
Sphagnum	*Bryophyta*	20	40
Dryopteris (shield fern)	*Pteridophyta*	72	144
Taxus (yew)	*Gymnospermae*	8	16
Pinus (pine)	*Gymnospermae*	12	24
Abies (fir)	*Gymnospermae*	16	32
Pisum (pea)	*Angiospermae*	7	14
Ribes (currant)	*Angiospermae*	8	16
Primula sinensis	*Angiospermae*	9	18
Primula kewensis	*Angiospermae*	18	36
Lycopersicum esculentum (tomato)	*Angiospermae*	12	24
Solanum nigrum (nightshade)	*Angiospermae*	36	72
Triticum monococcum	*Angiospermae*	7	14
Triticum durum	*Angiospermae*	14	28
Triticum vulgare	*Angiospermae*	21	42
Zea mays (corn)	*Angiospermae*	10	20
Carex aquatillis	*Angiospermae*	37	74
Musa sapientum	*Angiospermae*	8	16
Allium cepa	*Angiospermae*	8	16
Lilium	*Angiospermae*	12	24

* After Painter.

which can exhibit individuality either in appearance or in behavior.

Thus in each division by which the cells of the body are multiplied and by which growth and development proceed, there is an exact division of the chromatic material of the nucleus so that each cell receives the same complement of chromosomes, and presumably of the smaller units of which the chromosomes are composed.

Formation of the Germ Cells.—The usual result of mitotic cell division is the production of two cells exactly equivalent as regards the amount and kind of chromatin in their nuclei. When the mature animal or plant forms its reproductive cells, however, an important variation of this method is introduced, which is peculiar to the preparatory or *maturation* divisions of the gametes. The series of these maturation divisions by which the gametes are formed by the cells of the reproductive tissue and prepared for reproduction is known as *spermatogenesis* in the male and *oögenesis* in the female. (*Microsporogenesis* and *megasporogenesis* refer to the analogous processes in plants.) These processes are essentially similar in the two sexes, although because of the differences in the end products, numerous, small, often motile sperm or male cells, and fewer non-motile eggs containing stored food material—there are some secondary differences in the maturation of the gametes in the two sexes. As the simplest example of the maturation process the steps will be described by which the male gametes—spermatozoa—of the higher animals are formed.

Spermatogenesis (Fig. 52).—At a time preceding the sexual activity of the animal, in some cases by very long periods, there occurs in the testes of the male a series of cell divisions resulting in the formation of functional spermatozoa. The first step consists in the division of some of the cells (spermatogonia) lining the small tubules of which the testis is partly composed. By ordinary equational cell divisions the spermatogonia give rise to a second series of cells, the primary spermatocytes. These may divide to form cells like themselves, or may by a novel process give rise to other cells known as secondary spermatocytes, which give rise in turn to the gametes themselves. The chief and highly important difference between the primary and secondary spermatocytes is that the nuclei of the latter contain but *one-half as many chromosomes* (known as the *haploid* condition)

as occur in the primary spermatocytes or in other cells of the animal (known as the diploid condition). This halving of the characteristic number of chromosomes always introduces the formation of male and female gametes in animals and plants,

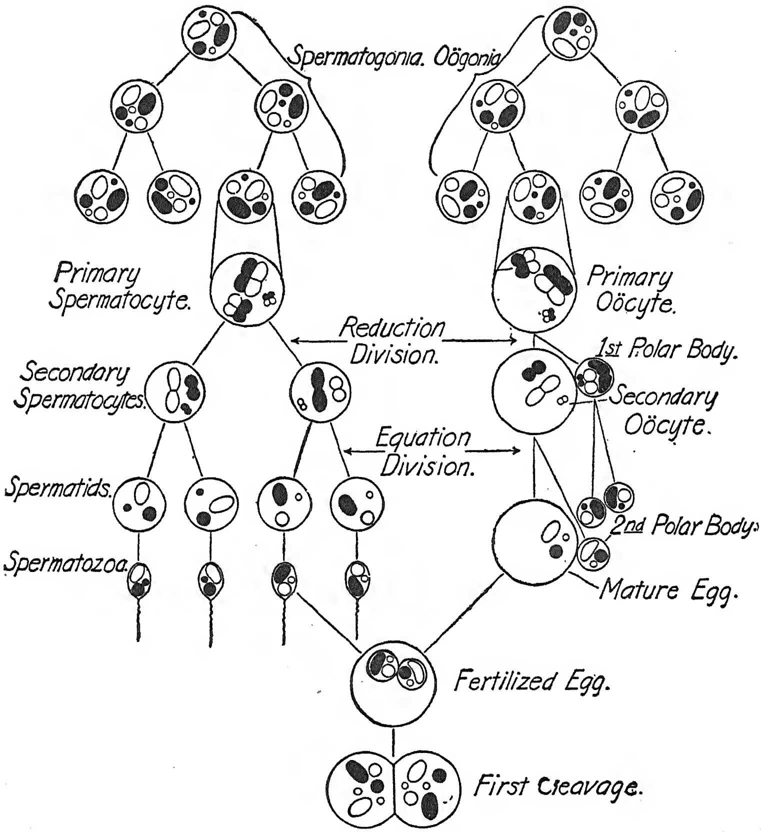


FIG. 52.—Diagram of spermatogenesis and oögenesis in an animal. (*After A. F. Shull.*)

and is brought about by a variation of the mitotic division known as the *reduction division.*

Reduction of Chromosomes.—The mechanism of the reduction division is illustrated in Fig. 53. In ordinary mitosis it has been seen that each chromosome splits longitudinally into two equal halves. In the reduction division the chromosomes do not

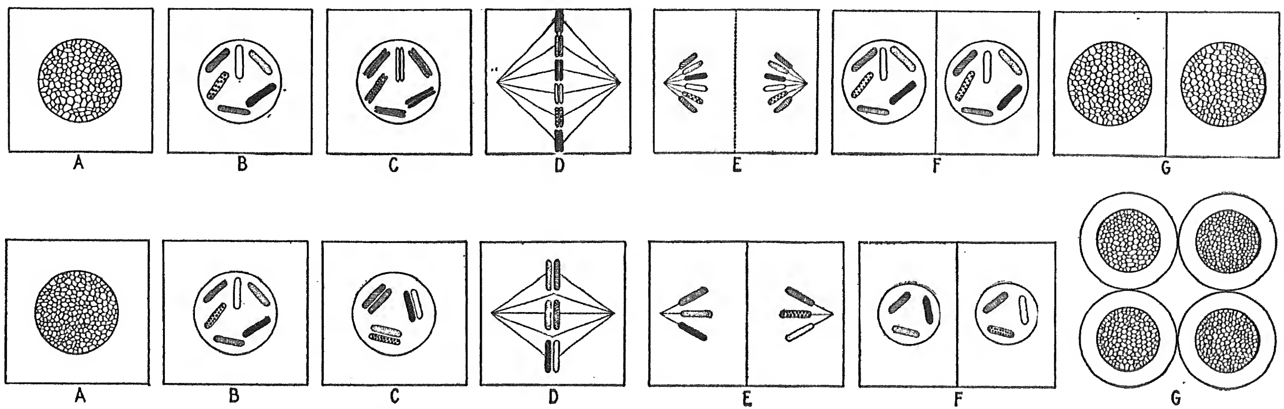


FIG. 53.—Comparison between mitosis in the body cells and in the reduction division which precedes the formation of the reproductive cells. The individual chromosomes are differently marked. In ordinary mitosis (upper row) it is evident that the chromatin is divided equally between the two daughter cells (*F* left and right). In the reduction division (lower row) the chromosomes do not split but align themselves in pairs (*C* and *D*) and one member of each pair goes to each pole (*E*), resulting in the formation of two cells (*F*), each with half as many chromosomes as the body cells. These by a subsequent equational mitosis give rise to four functional gametes (*G*). (*Modified from Sharp.*)

split but align themselves *in pairs,* of which one member subsequently passes to one pole and one to the other.[1]

The two members of each pair are known as *homologous chromosomes,* and investigation has shown that one member originally came from the male parent and one from the female. It is significant that the two members of a pair, or *homologues,* are usually similar in size, shape, and constitution and thus seem to be closely related to each other. The chromatic material of the nucleus should, therefore, be regarded not as a series of dissimilar and unrelated chromosomes but as a series of *pairs of similar chromosomes,* although this paired condition is evident only at the cell divisions preceding the formation of the gametes. It is further significant that not only does each gamete contain half the number of chromosomes of the body cells, but that it contains one member of every pair of homologous chromosomes. This at once suggests a parallelism between the behavior of chromosomes and of genetic factors which will be discussed later.

After the reduction division the primary spermatocytes undergo a single equational division resulting in the production of the *spermatids* which, by elongation and shifting of the nucleus, and addition of the headpiece and the tail or flagellum, become converted each into a mature spermatozoön.

Oögenesis (Fig. 52).—The maturation of the egg follows a similar course except that the reduction division, instead of resulting in two functional cells of equal size, gives rise to one large functional cell, the secondary oöcyte, and to one small degenerate cell, the first polar body. Each of these cells has the reduced number of chromosomes, and each subsequently divides equationally, the oöcyte to produce the large functional egg and another polar body; the first polar body into two polar bodies which disintegrate and disappear. Spermatogenesis produces

[1] It is probable that during pairing or *synapsis* the members of the pair may twist about each other and fuse at several points. It has been suggested that when they separate the chromosomes may break at the fusion points, and that the members of the pair may exchange parts so that each chromosome may come to be composed of parts of both members of the pair. This occurrence is made more probable by the genetic evidence on crossing over of factors from one chromosome to its mate (Chap. VII). In rare cases the two members of the pair fail to separate or disjoin but both pass together to one pole which has then one extra chromosome. This exceptional occurrence is known as *non-disjunction* and has important consequences in inheritance as shown in Chap. IX.

four small gametes of equal size from a single spermatocyte; whereas in oögenesis a single large egg and three small degenerate cells are formed from each oöcyte. The difference between maturation in the male and in the female is chiefly in the larger amount of food accumulated in the egg cell. The two processes are identical in their essential function of producing gametes with one representative of each of the parental pairs of chromosomes. Both spermatogenesis and oögenesis continue throughout the life of the individual whenever gametes are formed. They may be periodic in occurrence or may take place more or less continuously.

The Reduction Division in Plants.—Whatever the incidental complications, the essential feature of reduction of the chromatin by half obtains in both sexes in plants and animals. The results are always the same; that is, the gametes always contain one-half of the number of chromosomes characteristic of the parents, and one representative of each of the parental pairs.

On account of the complexity introduced by the alternation of generations previously described, plants differ from animals in the point in their life cycle at which the reduction division occurs. The sporophyte generation, like the animal body, has the double (diploid) number of chromosomes, but the entire gametophyte generation has the single (haploid) number. Reduction takes place in the formation of the spores (pollen grains and megaspores) by the sporophyte. Each spore mother cell contains the diploid chromosome number, but at its first division this is reduced to half. Each daughter cell divides equally into two, and these four cells become spores. The gametes, produced by the gametophyte, contain the same (haploid) chromosome number as do all the gametophytic cells, so that there is no reduction immediately preceding their formation, as is the case in animals.

Distribution of the Chromosomes in Development.—Fertilization and subsequent development take on a special significance when viewed as processes involving an exact method of chromosome distribution. Fertilization is essentially the union of two nuclei, each containing half of the number of chromosomes characteristic of the species. The single nucleus thus formed with the diploid or zygotic number of chromosomes gives rise by equational divisions to the nuclei of all of the cells of the body. "All the somatic (body) cells are qualitatively similar in chro-

matin content: they contain representatives or descendants of each and every chromosome present in the first cell of the series" (Sharp). In each body cell, therefore, half of the chromosomes trace from those derived from the father and half from those derived from the mother; and all chromosome characteristics are distributed equally to all of the cells of the body.

The Parallelism between the Behavior of Chromosomes and Genetic Factors.—In the last few paragraphs the steps have been described by which certain parts of the nucleus of animal and plant cells, the chromosomes, are distributed among the gametes. This process is not an hypothetical one but a description of fact, since it is founded on actual microscopic evidence. The point which must now be emphasized is that the behavior of the chromosomes, in the history of the formation of gametes and of fertilization, resembles in a very striking way the behavior of the units of inheritance, the genetic factors, as inferred from the breeding evidence. The truth of the assumptions concerning the behavior of the factors (Mendel's laws) is convincing, not because the factors in the gametes have been seen, but because the principles of segregation and independent assortment are the only hypotheses which satisfactorily explain the results of breeding experiments. The parallelism to be noted, then, is that which exists between a concrete set of facts (chromosome behavior) and the hypotheses proposed to explain another set of facts (factor behavior). Aside from the general similarity between these two processes in the mathematical regularity with which each seems to take place, there are certain specific laws which apparently apply in a similar way to each.

1. Both the chromosomes and the factors behave in inheritance as though they were individual units. The individuality of the chromosomes is a matter of direct observation under the microscope. Each pair of chromosomes can be seen, in favorable preparations, to be different from every other pair. Each factor, likewise, has an individuality which is inferred from its indivisibility in inheritance and its emergence intact and unaltered after a cross.

2. The facts of inheritance can be explained only on the assumption that the genetic factors which make up the genotype of every individual occur in *pairs* (allelomorphic pairs) and that one member of each pair was contributed by one parent of this individual and the other by the other parent. This is

precisely the situation observed in the case of the chromosomes, for these are also seen to be definitely associated in pairs, the members of which have been derived from the two parents.

3. Each gamete is seen to contain only one member of each pair of chromosomes, and each gamete likewise can contain but one member of each pair of allelomorphic factors. That the gametes contain the reduced or haploid number of chromosomes is known from actual chromosome counts, especially at the reduction division. That each gamete contains only one of a pair of factors was found to be a necessary inference from breeding experiments. In fact, the most important of Mendel's principles assumes a process known as *segregation*, whereby, in the formation of gametes, each factor separates sharply from its alternative or allelomorph, the two members of the pair always entering different gametes so that the gametes are "pure" genetically. Such a separation is actually found to take place between the two members of a pair of chromosomes at the reduction division, resulting in the inclusion of each member of the pair in different daughter cells (gametes). Both factors and chromosomes, then, undergo segregation, and in respect to both each gamete is pure, containing only one member of a pair.

4. The various pairs of chromosomes are assorted or distributed to the gametes independently of each other. A careful study of the diagram in Fig. 54 will show that the principle of independent assortment applies to chromosomes in precisely the same way in which it has been assumed that it applied to genetic factors. It seems to be merely a matter of chance to which pole a given member of a chromosome pair goes in the reduction division, so that it is also a matter of chance as to whether a given member of a pair happens to become associated with one or with the other member of another chromosome pair. This is precisely the manner in which factors behave in inheritance, for in the formation of gametes by individuals heterozygous for two or more factor-pairs, it is purely a matter of chance as to how the members of the various pairs happen to become assorted and associated in the gametes, and segregation in one factor pair is entirely independent of that in every other.

Many of these items of similarity were noted soon after Mendel's law was rediscovered, and even before that time the chromosomes had often been regarded as the most probable carriers of the genetic factors. This assumption, however,

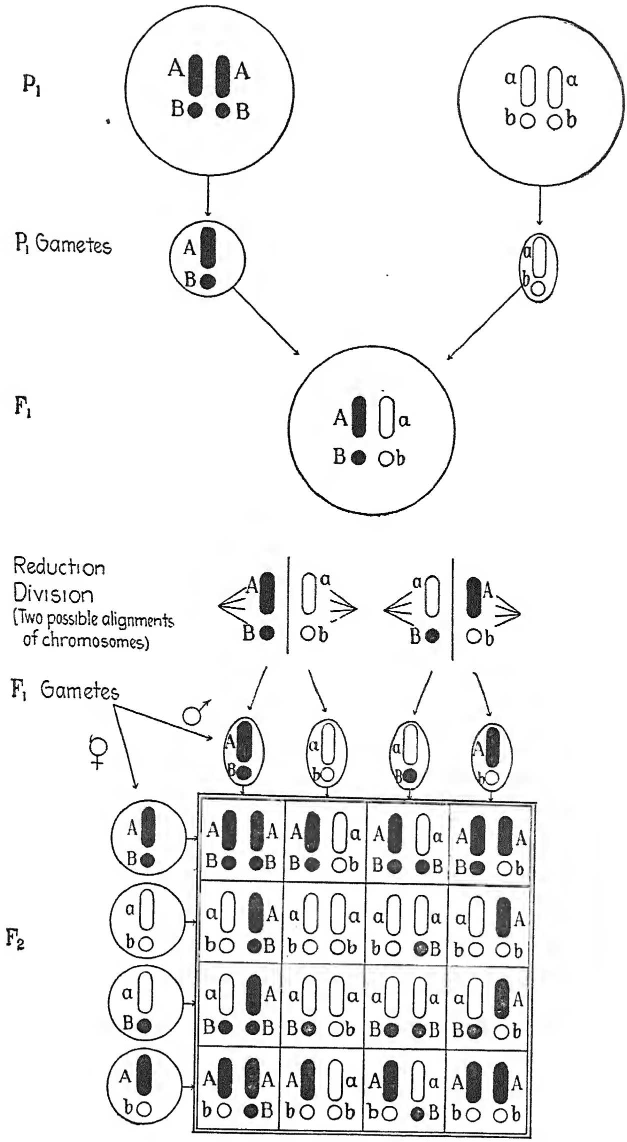


FIG. 54.—Diagram showing independent assortment of two pairs of chromosomes, *A-a* and *B-b*. Note that at the reduction division there are *two* possible alignments of chromosomes producing *four* types of gametes. By random union these produce the sixteen different chromosome combinations shown in the F_2 checkerboard.

would have remained largely a speculation, and the evident parallelism between the factors and the chromosomes would have been merely an interesting resemblance, if direct proof of an entirely different sort had not been brought forward. The greatest advance in genetics in recent years has been the discovery and development of the proof that the factors are indeed located in, and are definite parts of, the chromosomes. The next two chapters discuss, therefore, the chromosome theory of inheritance and the facts of *linkage* which support this theory.

QUESTIONS FOR THOUGHT AND DISCUSSION

59. In what important particular does sexual union at fertilization differ from the union of tissues in grafting or tissue-transplantation?

60. Of what advantage do you think it has been, for the male and female gametes, in the evolution of sex, to have become so different from each other, the former tending to be small and motile and the latter large and non-motile?

61. What do you think it is which causes the sperm to approach and enter the egg?

62. What explanation can you suggest for the presence of polar bodies in the development of the animal egg?

63. Wherever parthenogenesis (the development of a gamete without union with another gamete) occurs among animals, it is always the female gamete which has this power. Why do you suppose this is so?

64. If a character is found to be inherited only through the mother, in what part of the gamete is it probably transmitted?

65. If the germ cells were formed by direct division of the nucleus without mitosis, how would this affect the character of the gametes and the process of inheritance?

66. What would happen to the chromosomal constitution of the nucleus if the reduction division did not take place?

67. What do you think would happen in the gametogenesis of a species with an *odd* number of chromosomes?

68. What probable advantage may there have been, originally, in the existence of an alternation of generations?

69. Why has such a complicated system of accessory reproductive structures as the calyx and corolla been developed in plants?

70. Do you think that the characteristics of the fruits of an apple tree will be affected by the source of the pollen which fertilized the flowers? Explain.

71. What important difference is there between animals and plants in the method of bringing the male and female gametes together, and to what fundamental difference between these two groups of organisms is this due?

72. If half of the chromosomes of an oöcyte pass into the first polar body (which degenerates), why are not some of the chromosomes lost entirely in the process of oögenesis in animals?

73. In some groups of animals and plants the chromosome number of one species is a multiple of that in another. Thus in wheat some species have fourteen, some twenty-eight, and some forty-two chromosomes. What does this suggest as to the evolutionary history of these species?

74. In the Drosophilidae (the family to which the fruit fly belongs) Metz has found that some species have eight chromosomes while other related species have six, eight, ten, and twelve chromosomes each. Assuming that all species are descended from an eight-chromosome type, how would you account for the species with more and with fewer chromosomes?

75. What reasons are there for believing that every cell in the body contains the full complement of genetic factors that are present in the fertilized egg?

76. If this belief is correct, how do you think it is possible for the differentiation of specific tissues and organs to take place during development?

77. In the rather rare cases where two species can be successfully crossed, as the horse and the ass, the hybrids produced are almost always sterile. From what you know of chromosome behavior, what explanation can you suggest for this fact?

PROBLEMS

127. At the time of synapsis preceding the reduction division, the homologous chromosomes align themselves in pairs and one member of each pair passes to each of the daughter nuclei (page 141). Assume that in an animal with four pairs of chromosomes, chromosomes A, B, C, and D have come from the father and A', B', C', and D' have come from the mother. In what proportion of the germ cells of this animal will all of the paternal chromosomes be present together? all of the maternal?

128. If a given character, A, pertains to the *gametophyte*, and the gametophyte of one plant shows it while that of another plant shows its allelomorph a; and if gametes from these two gametophytes unite, what will be the appearance of the succeeding generation of gametophytes with respect to this character?

129. If one gametophyte displays characters A and B and is crossed with another which displays a and b, what will the next gametophyte generation look like with respect to these two characters?

130. In the honey bee, unfertilized eggs may develop by parthenogenesis, in which case they produce males (drones). The fertilized eggs produce females (workers or queens). In spermatogenesis in bees there is no reduction division. If the females contain thirty-two chromosomes in the body cells and if oögenesis is the same as in other species, how many chromosomes would you expect to find in the body cells of the males?

131. A queen bee heterozygous for a dominant character mates with a drone which shows the same character. What characters would you expect the male and female offspring to show?

REFERENCE ASSIGNMENTS

38. What explanations have been offered for the evolution of sex?

39. What is meant by parthenogenesis? Give an example from animals and from plants.

40. What important differences are there between a typical animal cell and a typical plant cell?

41. Who discovered the existence of the process of mitotic cell division?

42. What is the chemical nature of chromatin?

43. What is known of the structure of the chromosome?

44. Look up the chromosome number in ten different species of animals and plants not included in the list in your text.

45. What evidence is there that the chromosomes retain their individuality in the resting nucleus?

46. Describe the process of *double fertilization* in angiosperms.

47. In corn breeding it has been found that the pollen has an immediate effect on some characters of the seed which it fertilizes. This effect is known as *Xenia*. What causes it? What kind of seed characters does it affect? Describe the inheritance of a character showing Xenia.

48. Give the derivation of the following terms and explain in what way each is appropriate:

Gamete
Spermatogenesis
Oögenesis
Sporophyte
Synapsis
Chondriosome
Haploid
Diploid
Gametophyte
Chromosome
Mitosis

CHAPTER VII

LINKAGE

The principle of independent assortment, which, as has been seen in the preceding chapters, governs the behavior both of genetic factors and of chromosomes, has been supported by the results of breeding experiments with all sorts of animals and plants during the past quarter of a century. Soon after the rediscovery of Mendel's laws some doubt began to be cast on the universal applicability of this principle, since it did not explain certain exceptional results. The increasing frequency with which such exceptions were observed and the more careful study given them led to the formulation of a new principle of inheritance, the principle of *linkage*. This is the hypothesis which the American zoölogist, Prof. T. H. Morgan, originally devised to explain such exceptions, and its further development has since led to a general revision and clarification of our views as to the physical basis of inheritance, the nature of factors and even of protoplasm itself.

Coupling and Repulsion.—The first case of what is now called linkage was discovered in 1906 by the English investigators Bateson and Punnett, in the course of their studies of inheritance in the sweet pea. In one of their experiments two races of sweet peas were crossed, one having purple flowers and forming long pollen grains and the other having red flowers and round pollen. Purple, P, they found to act as a simple dominant to red, p, while long pollen, L was dominant to round, l. Each trait segregated from its allelomorph in a normal 3:1 ratio in F_2. But instead of finding, as they expected, that these two characters were assorted independently of one another to produce an F_2 ratio of nine-sixteenths long-pollened purple, three-sixteenths long-pollened red, three-sixteenths round-pollened purple, and one-sixteenth round-pollened red, they obtained the F_2 ratio below (data from Punnett 1923):

P_1 Purple, long × Red, round

F_1 Purple, long

F_2	Purple, long	Purple, round	Red, long	Red, round	Total
Actual numbers	4,831	390	393	1,338	6,952
Expected numbers	3,910.5	1,303.5	1,303.5	434.5	6,952
Expected ratio	9/16	3/16	3/16	1/16	

The numbers obtained were obviously very different from those expected on the assumption that flower color and pollen shape assorted independently. The chief peculiarity of the result was that the combinations of traits which occurred in the parents (purple flowers with long pollen and red flowers with round pollen) appeared much *more* frequently than they should have while the *new* combinations or recombinations of characters different from those introduced by the parents (purple with round and red with long) appeared *less* frequently than expected. If these factors were inherited independently, there should have been 4,345 F_2 plants showing the parental combinations; actually there were, 6,169; while instead of the 2,607 new combinations expected, there were only 783. It appeared to the experimenters that the factors for purple and long had tended to stay together in inheritance, and they called this phenomenon the "coupling of factors." Later the same characters were involved in a cross similar to the above, except that the factors for flower color and pollen shape were differently associated in the two parents, purple and round entering the cross from one parent, and red and long from the other. The results of such a cross are given below, compared with those which would be expected if *P-p* and *L-l* are inherited independently.

P_1 Purple, round × Red, long

F_1 Purple, long

F_2	Purple, long	Purple, round	Red, long	Red, round
Actual	226	95	97	1
Expected	235.8	78.5	78.5	26.2

Here again it is found that the parental types (purple round and red long) are too numerous, for there are 192 of them instead of the 157 expected, while of the new combinations there are only 227 instead of the 262 expected. Apparently, the F_1 plants produced more of the parental types of gametes *Pl* and *pL* than of the types *PL* and *pl*, instead of the equality of all four types which should have resulted if the factors assorted independently. From this the investigators inferred that the factors introduced by different parents showed an aversion to entering the same F_1 gamete. They called this tendency "repulsion." The two tendencies, coupling and repulsion, were evidently similar in effect, for both resulted in the formation of an excess of the parental combinations of factors and a deficiency of the new type of combinations.

These cases of coupling and repulsion remained for several years as outstanding exceptions to Mendel's principle of independent assortment. About 1910, however, many additional cases of this type of inheritance were discovered by Morgan in the fruit fly, *Drosophila*. He saw that both coupling and repulsion were examples of a single phenomenon which he termed *linkage*, or the tendency of factors to remain in their original combinations in inheritance. He suggested that such a result would follow if the factors which showed linkage with one another were located *in the same chromosome*, and hence tended to be inherited as a *block*, rather than independently of one another as Mendel had supposed. This idea soon gathered additional support from the data which Morgan and his co-workers, Bridges, Muller, Sturtevant, and others, obtained from breeding experiments and cytological study in the fruit fly. From such data in the succeeding ten years the chromosome theory of inheritance was formulated, and many of the details of the physical basis of heredity were described and explained. The chromosome theory, together with some of the evidence from *Drosophila* which supports it, will be discussed more fully in the next chapter, while the remainder of this one will present and explain typical cases of linkage in different animals and plants.

Linkage.—It has already been shown by examples from sweet peas that certain factors do not assort independently after a cross but tend to remain in the same combinations in which they entered it. It is not evident from the examples cited what causes this tendency. To make the matter clear it will be

necessary to consider a case of linkage in detail, and especially to trace the behavior of the factors during the critical stage of the formation of the gametes of the dihybrid when assortment of factors takes place. From what has been learned of this process in Chap. IV it would be expected that the combinations of factors in the gametes from a double heterozygote (such as *Aa Bb*) would be best determined by back-crossing it to the double recessive, *aa bb*. The gametes of the heterozygote, *AB*, *Ab*, *aB*, and *ab*, unite in this case only with recessive gametes *ab*; and the appearance of the offspring *Aa Bb*, *Aa bb*, *aa Bb*, and *aa bb* provides an accurate indication of the genetic constitution of the gametes of the heterozygous parent, since each dominant factor in the progeny is directly traceable to the gamete in which it was contained. In an F_2 generation from *Aa Bb*, on the other hand, the individuals containing both dominant factors may be traceable either to unions of *AB* gametes with *ab*, or of *Ab* with *aB*, and so on. The assortment of factors in the gametes of the hybrids is obscured by dominance, and the F_2 ratio, therefore, does not give a direct index of the kinds of gametes produced by the F_1. For this reason cases in which linkage is suspected are usually investigated by crossing individuals heterozygous for the factors involved with individuals recessive for these factors.

Linkage in Corn.—A clear case of linkage in corn has been investigated in this way by Hutchison. The difference between colored and colorless seeds in this plant may depend on a single factor pair (*C*, colored; *c*, colorless). Colored acts as a simple dominant to colorless. Similarly with regard to the character of the endosperm or the part of the seed which contains the food stored up for the embryo, a single factor has been found to differentiate a type in which the endosperm is full or plump from one in which it is shrunken or indented. Full, *S*, is dominant to shrunken, *s*. When a plant with colored, full seeds is crossed with a plant with colorless, shrunken seeds, the F_1 seeds are colored and full. As in the example from sweet peas, an F_2 raised from this F_1 fails to exhibit the 9:3:3:1 ratio which it is customary to expect from a dihybrid. Instead of such a ratio it is found that nearly all of the F_2 seeds are either colored and full as in one parent, or colorless and shrunken as in the other. The new combinations, colored with shrunken and colorless with full, are not found in normal proportions. It is, therefore, evident

that the factors for seed color and endosperm character are linked.

In order to test this linkage Hutchison crossed a colored, full-seeded plant with a colorless, shrunken-seeded one. A large number of F_1 colored, full plants (*Cc Ss*) were then back-crossed to the double recessive type, colorless, shrunken (*cc ss*). It would be expected, on the principle of independent assortment, that the F_1 would form four kinds of gametes *in equal numbers*, *CS*, *Cs*, *cS*, and *cs*, and that when united with gametes of the type *cs*, from the double recessive, the following kinds of progeny would be produced *in equal numbers:*

Colored, full	*Cc Ss*
Colored, shrunken	*Cc ss*
Colorless, full	*cc Ss*
Colorless, shrunken	*cc ss*

When the cross was made, however, this expectation was not realized, but the following result was obtained (data from Hutchison 1922):[1]

P_1 Colored, full × colorless, shrunken
(*CS*) (*CS*) | (*cs*) (*cs*)
F_1 Colored, full

F_1 Colored, full × colorless, shrunken
(*CS*) (*cs*) | (*cs*) (*cs*)

	Back-cross Progeny			
Colored, Full	Colored, Shrunken	Colorless, Full	Colorless, Shrunken	Total
(*CS*) (*cs*)	(*Cs*) (*cs*)	(*cS*) (*cs*)	(*cs*) (*cs*)	
4,032	149	152	4,035	8,368

The parental combinations (colored, full and colorless, shrunken) are *more numerous* than expected, while the recombinations (colorless, full and colored, shrunken) are correspondingly *less numerous* than expected (Fig. 55). This inequality in the progeny of the back-cross proves the existence of a similar inequality in the gametes of F_1. Instead of being produced in equal numbers, these must have been formed as follows:

[1] In representing the genotype in which the factors are linked, it is customary to indicate this by enclosing the linked factors in parentheses, or by other means. Thus a colored, full, dihybrid, instead of being represented by *Cc Ss*, would better be expressed (*CS*) (*cs*) or (*Cs*)(*cS*), depending on the combination in which the factors entered the cross.

Parental combinations.....	*CS*	4,032
	cs	4,035
		8,067, or about 96.4 per cent of the total gametes tested.
New combinations........	*Cs*	149
	cS	152
		301, or about 3.6 per cent of the total gametes tested.

Under independent assortment these two classes of gametes would each have comprised 50 per cent of the total. It is obvious then that the two factor pairs, *C-c* and *S-s*, have not assorted independently, and it may be said that they are *linked* together.

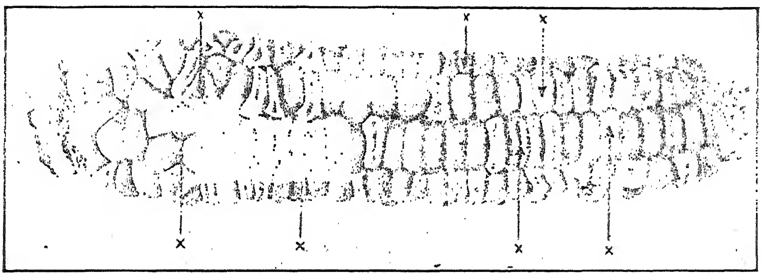


FIG. 56.—The kernels on this ear show linkage of factors for aleurone color and for shrunken endosperm. It resulted from the cross of a heterozygous plant (which had received the factors for *colored and full* from one parent and for *colorless and shrunken* from the other) with a double recessive colorless, shrunken plant. Most of the kernels are colored and full or colorless and shrunken (non-crossovers) and a few have the new combinations *colored shrunken* and *colorless full*. Such crossover seeds are designed by x. (*From Hutchison, in Journal of Heredity.*)

The indication of linkage is always some evidence, like the above, of departure from the ratio expected on the theory of independent assortment.

One step, therefore, in the explanation of linkage is the discovery of the fact that the *gametes of a plant or animal which is heterozygous for two linked traits are not formed in equal numbers but that the gametes with the parental combinations of factors are always more numerous than the gametes with the new combinations of factors*. This fact holds good for all pairs of linked characters, no matter in what combination they enter a cross. In the first illustration the factors *C-c* and *S-s* entered the cross in the combinations *CS* from the colored, full parent and *cs* from the color-

less, shrunken parent, and these combinations tended to remain intact; but in another experiment the original parents were colorless, full and colored, shrunken. The F_1 was, of course, the same in appearance as in the previous cross and this was back-

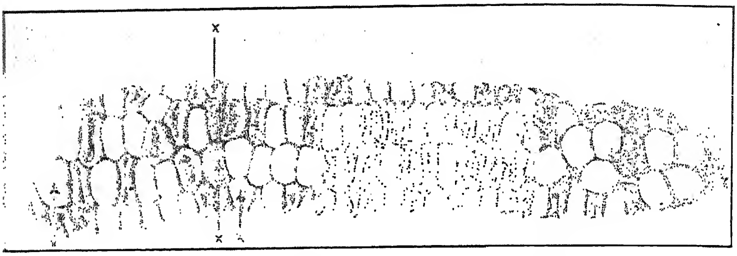


FIG. 56.—An ear of similar ancestry to that on preceding page (Fig. 55) except that the factors entered the F_1 plants in different combinations, *colored and shrunken* coming together from one pure parent and *colorless and full* from the other. The crossovers (x) in this case are *colored full and colorless shrunken*. (*From Hutchison, in Journal of Heredity.*)

crossed to the double recessive. The progeny of this cross showed (Fig. 56) an excess of colorless, full and colored, shrunken kernels—*the parental combinations*—as shown below:

P_1 Colorless, full × colored, shrunken
(cS) (cS) | (Cs) (Cs)
F_1 Colored, full

F_1 Colored, full × colorless, shrunken
(cS) (Cs) | (cs) (cs)

BACK-CROSS PROGENY

COLORED, FULL	COLORED, SHRUNKEN	COLORLESS, FULL	COLORLESS, SHRUNKEN	TOTAL
(CS) (cs)	(Cs) (cs)	(cS) (cs)	(cs) (cs)	
638	21,379	21,906	672	44,595

Whatever the parental combinations may be, linkage tends to keep them intact.

The best explanation of linkage which has been proposed is based on the assumption that linked factors are located *in the same chromosome*. It has been shown above that at the reduction division one member of each pair of chromosomes of the parent goes into each gamete which is formed. If, then, two factors such as c and s are present in one chromosome of the parental plant, these should be inherited together and should follow

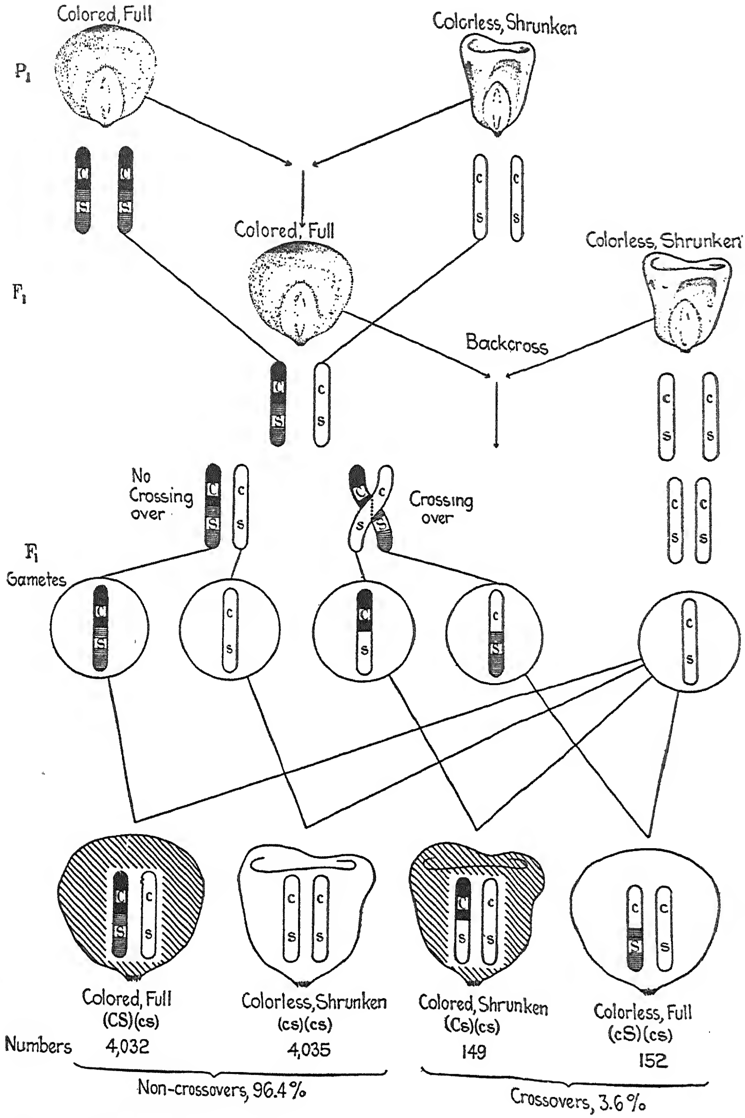


FIG. 57.—Diagram showing the chromosome explanation of linkage and crossing over in corn. The history of the genes for colored-colorless (C-c) and full-shrunken (S-c) and of the chromosomes in which they are located is traced through a cross between two pure types and the backcross of F_1 with a double recessive. (*Data from Hutchison.*)

binatio.

same course as the chromosome which bears them. The history of the chromosomes carrying these two genes[1] is shown in Fig. 57.

Crossing-over.—If two genes are located in the same chromosome, however, and the chromosome remains intact in inheritance, the two factors should remain together in *all* cases, or, in other words, linkage should be complete. This is not what happens, for linkage is apparently always partial, the linked factors sometimes separating. In the example cited above, the factors held together in about 97 per cent of the cases but broke apart in about 3 per cent. In other crosses two genes have been found to remain together in nearly all the gametes, as, for instance, in rats, where the gene for albinism and a gene for yellow coat remain together in over 99 per cent of the F_1 gametes and separate in less than 1 per cent; or the genes may separate in *nearly* 50 per cent of the cases, as in the fruit fly, where two genes called "star" and "speck" are associated in 52 per cent and separate in 48 per cent of the gametes. Those cases in which linked factors break apart from their original combinations (that is, in which genes originally separate become united in one gamete or individual, or in which genes originally together become separated) are known as new combinations or *cross-overs*. Under independent assortment the original combinations, or non-cross-overs, and the new combinations, or cross-overs, are approximately equal in number. Under linkage, the non-cross-overs are always *more numerous* than the cross-overs. Linkage may vary greatly with different genes, producing all the way from slightly over 50 per cent to nearly 100 per cent of non-cross-overs.

The physical mechanism by which new combinations of linked genes takes place is known as *crossing-over*. If it is believed that genes which exhibit linkage do so because they are located in the same chromosome, then it must be assumed that breaks in this linkage (cross-overs) result from an *interchange of parts* between members of the same pair of chromosomes, by which two genes, originally located in one chromosome, may be separated and come to lie in different ones (as shown in Fig. 58). In the formation of the germ cells of the hybrid the two chromosomes of a pair always pass to different gametes, so that the genes which have crossed over appear in different individuals among

[1] The more modern terminology developed under the chromosome hypothesis is here employed and factors referred to as *genes*.

the progeny. The time at which crossing-over occurs is probably at that stage in the maturation of the germ cells known as *synapsis*, just preceding the reduction division. At this period the members of each pair of chromosomes seem to be mutually attracted and come to lie side by side, often twisting loosely about one another. This process of synapsis or conjugation provides just the opportunity for an exchange of material between homologous chromosomes which our assumption requires.

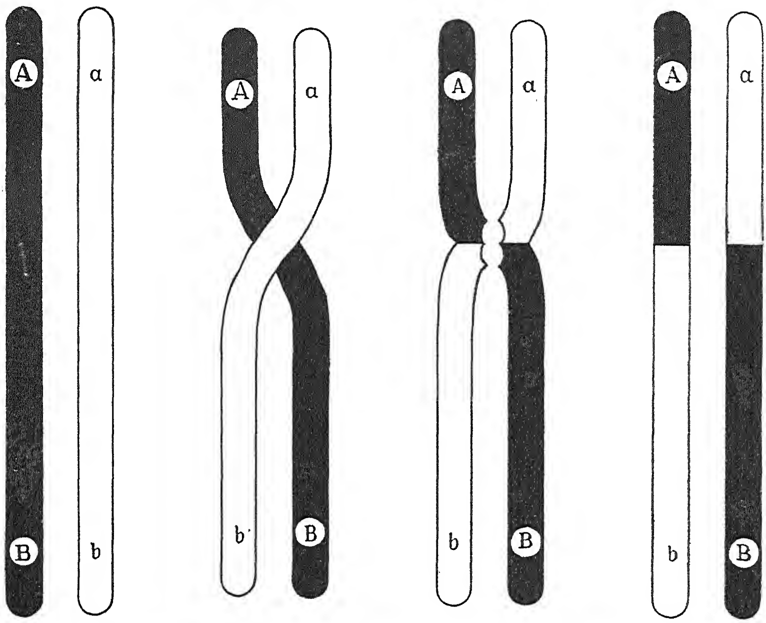


Fig. 58.—Diagram showing the mechanism of crossing over between two genes, *A* and *B*, in the same chromosome.

The genetic evidence shows that this exchange probably comes about by the breaking of the twisted conjugating chromosomes at the points where they cross one another, and that this break is followed by the union of a whole piece of one chromosome with the reciprocal piece of the other. The result is that although each pair of the chromosomes enters synapsis intact, they may emerge as composite structures, one part (or more), with all its constituent genes, having come from the mother and the other from the father. Such a process of crossing-over probably takes place in normal inheritance, but becomes noticeable only

when the parts of the chromosome contain *different* genes for visible traits, as in the formation of gametes by animals or plants heterozygous in two or more linked factors.

Linkage, then, is the tendency for genes to remain in their original combinations in inheritance due to their residence in the same chromosome; while crossing-over is the tendency for linked genes to break apart. Crossing-over explains why linkage is not complete.

The Measurement of Linkage.—Linkage occurs in different degrees and is thus a quantitative phenomenon which may be measured by the amount of crossing-over which occurs. If there is but little crossing-over between two genes, it is said that the linkage is strong or close; if there is much, it is said that linkage is weak or loose. The usual method of measuring linkage is, therefore, to cross an animal or plant which is heterozygous for the linked genes, such as (*CS*) (*cs*), with the double recessive (*cs*) (*cs*), and to count the numbers of individuals in which the two genes remain in their original parental combinations (the non-cross-overs) and the individuals in which the two genes have formed new combinations (the cross-overs). The strength of linkage is then expressed as the cross-over value, or the percentage of cross-overs in the total number of progeny. Thus in the example used (page 154) the total number of individuals observed was 8,368, of which the cross-overs numbered 301 (149 + 152), or about 3.6 per cent of the total. The genes for colorless and shrunken or their allelomorphs, colored and full, are therefore said to be linked, with a cross-over value of 3.6 per cent. It should be remembered, of course, that linkage strength varies *inversely* as the cross-over value.

The degree of linkage between two given genes is constant for a given set of conditions, and once it is accurately measured, it may be *made the basis of prediction* for the behavior of these genes in subsequent breeding operations, regardless of the way in which they enter the cross (whether together or apart). Knowing the character of the gametes formed by an individual heterozygous for two linked genes, it is possible to predict what the offspring of this individual will be, when it is crossed not only with a double recessive but with any other individual. This can perhaps best be explained by using a somewhat simpler case than that of the corn problem. Assume, for example, that two genes *A* and *B* are linked with a cross-over value of 20 per

cent. If a homozygous AB individual is crossed with an ab one, the F_1, (AB) (ab), will form the following gametes:

$$\left.\begin{array}{l}40 \text{ per cent } AB\\ 40 \text{ per cent } ab\end{array}\right\} \ldots \text{ 80 per cent non-cross-overs}$$

$$\left.\begin{array}{l}10 \text{ per cent } Ab\\ 10 \text{ per cent } aB\end{array}\right\} \ldots \text{ 20 per cent cross-overs}$$

Now if it is desired to determine the appearance of the F_2 from the cross $(AB)(ab) \times (AB)(ab)$, a checkerboard may be constructed in the usual way *except* that the four types of gametes must be weighted by multiplying them by their relative frequencies, for they are not now equal in numbers (as in independent assort-

	4 AB (40 %)	1 Ab (10 %)	1 aB (10 %)	4 ab (40 %)
4 AB (40 %)	16 (AB) (AB)	4 (AB) (Ab)	4 (AB) (aB)	16 (AB)(ab)
1Ab (10 %)	4 (AB) (Ab)	1 (Ab) (Ab)	1 (Ab) (aB)	4 (Ab) (ab)
1 aB (10 %)	4 (AB) (aB)	1 (Ab) (aB)	1 (aB) (aB)	4 (aB) (ab)
4 ab (40 %)	16 (AB) (ab)	4 (Ab) (ab)	4 (aB) (ab)	16 (ab) (ab)

Fig. 59.—Checkerboard showing the expected composition of the F_2 from a cross between individuals differing in two linked genes A-a and B-b, which show 20 per cent of crossing over.

ment), but those of the type AB are four times as numerous as those of the type Ab, for example. In determining the number of offspring produced by a given gametic combination, therefore, the frequency of one type of gamete must be multiplied by the frequency of the other. The sixteen combinations will thus not be equal in number, but some will be represented by more individuals than others. The F_2 in the example is worked out in the checkerboard in Fig. 59. By adding together all the individuals of each visibly similar group, the F_2 will be found to consist of

66 per cent which appear AB, 9 per cent Ab, 9 per cent aB and 16 per cent ab. For determining cross-over percentage from an F_2 ratio, see Table VII at the end of this chapter.

The amount of crossing-over, or linkage strength, is also used in determining the location of genes in the chromosomes, since it may be assumed that the frequency of crossing-over is proportional to the distance between the genes. Genes which seldom cross over are assumed to be so near together that a break in the chromosome is not likely to occur between them; while those which cross over more frequently are assumed to be farther apart. This is explained at greater length in the next chapter, but is mentioned here because of its bearing on the chromosome explanation of allelomorphism which follows.

Complete Linkage.—The examples used have all been drawn from cases of partial or incomplete linkage, in which crossing-over occurs with measurable frequency. There are a number of cases, however, in which linkage appears to be complete, so that the genes always remain in their original combinations. This may be due to the absence of crossing-over under special conditions, or it may mean that the genes are so near together in the chromosome that a break never occurs between them.

Examples of the first type are very common in experiments with *Drosophila*, since in this fly it has been found that crossing-over rarely or never takes place in the germ cells of the *male*. Thus if a gray-bodied, vestigial-winged fly is crossed with a black-bodied, long-winged one, the F_1 generation is found to consist entirely of gray-bodied, long-winged flies. If one of the F_1 *males* is crossed to the double recessive type (a black-bodied, vestigial-winged female), only two kinds of offspring are produced, gray vestigial and black long (Fig. 60). The expected types of cross-overs—gray long and black vestigial—do not appear at all. If, however, an F_1 *female* fly is crossed with a black vestigial male, the four expected types (Fig. 61) are produced in the following proportions (data from Morgan, 1919):

Non-cross-overs		Cross-overs	
Gray vestigial	Black long	Black vestigial	Gray long
41.5 per cent	41.5 per cent	8.5 per cent	8.5 per cent
83 per cent		17 per cent	

Crossing-over therefore occurs in about 17 per cent of the gametes. The second experiment shows that a perceptible

distance separates the genes for black and vestigial and that absence of cross-overs in the gametes of the male is not due to the extreme closeness of the genes in the chromosome. It must be due, then, to conditions peculiar to the male, such as the

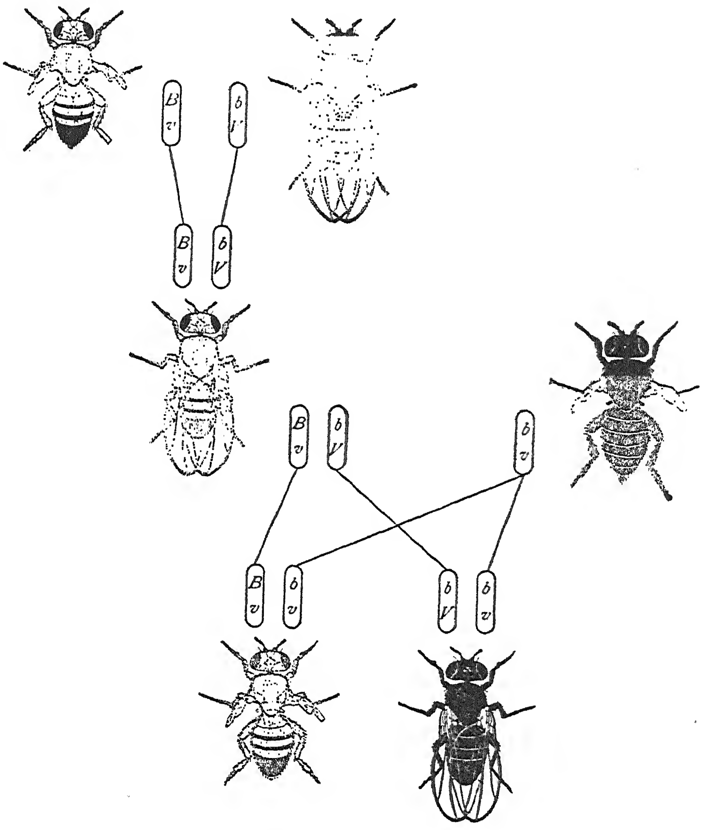


FIG. 60.—Complete linkage (no crossing over) in the male of *Drosophila*. Results of a cross between a gray, vestigial male and a black, long female; and of a backcross of the F_1 *male* with a black, vestigial female. Note that the offspring of this backcross are all like the original parents and that there are no cross-overs. (*From Morgan, Sturtevant, Muller and Bridges, courtesy Henry Holt and Co.*)

non-occurrence of synapsis or interchange of parts in spermatogenesis. Only two animals are known in which linkage is always complete in one sex; in *Drosophila* it is so in the male, and in the silkworm moth in the female. In other animals and plants for

which there is sufficient evidence, crossing-over is found to occur in both sexes.

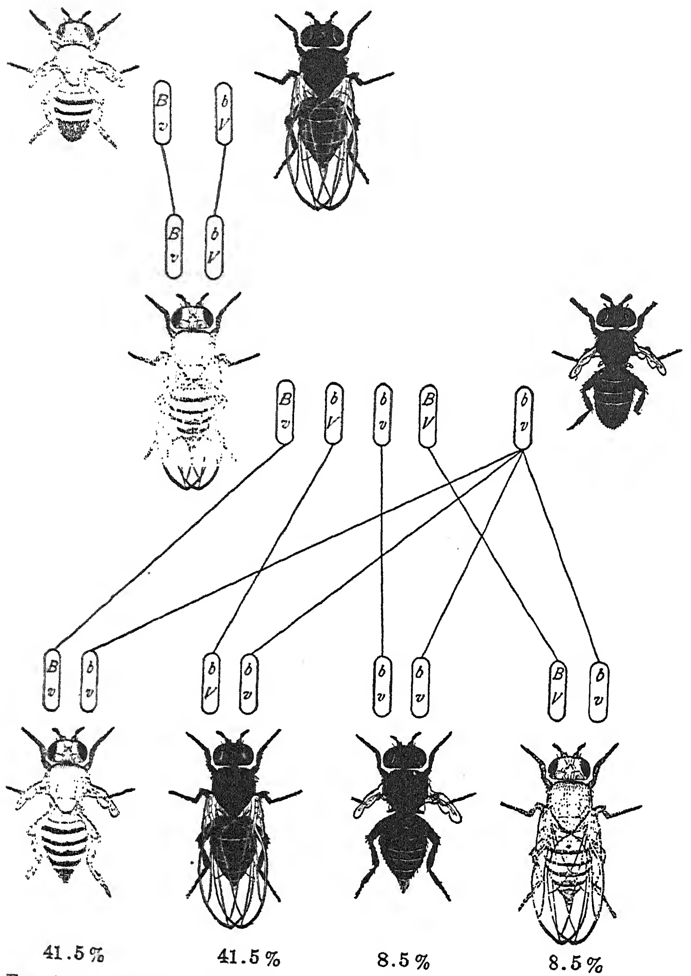


FIG. 61.—Crossing over in the female of *Drosophila*. Results of a cross between a gray, vestigial male and a black, long female; and of a backcross of the F_1 female with a black, vestigial male. (*From Morgan, Sturtevant, Muller and Bridges, courtesy Henry Holt and Co.*)

Theoretically, cases of complete linkage should be possible in which genes do not separate because they are so close together in the chromosome that a break cannot occur between them. Actual instances which might be explained in this way are rare

or may not occur at all; since all linked genes for which there is critical evidence do cross over in some cases. Although this may occur only once in many hundreds of instances, genes apparently are never so near together that no crossing-over is possible between them.

Multiple Allelomorphs.—What might seem to be cases of complete linkage between two genes may be better explained by the assumption that the genes which show no crossing-over are allelomorphs. It has already been pointed out that the relation between allelomorphs is such that one and only one ever enters the same gamete. This is what would be expected if the two allelomorphs were located in a pair of homologous chromosomes. Furthermore, allelomorphic genes must be exactly opposite each other in their respective chromosomes; otherwise, both might occasionally get into the same gamete by crossing over, a result which never occurs. Now there are some cases in which, instead of *two* allelomorphs, there are *several*, producing visibly different effects, which behave as though they were completely linked, but only one of them is ever present in any single gamete. One of the first and clearest of these cases was found in breeding experiments with rabbits. The common pink-eyed white (albino) rabbit (Fig. 62, bottom) has long been known to act as a simple recessive to the colored type (Fig. 62, top). Crosses of colored and albino rabbits produce only colored young, which when inbred give colored and albino progeny in the ratio of three-fourths colored to one-fourth albino. Color and albinism thus form a pair of allelomorphs. There is another form of albinism in rabbits, however, known as Himalayan albinism. Himalayan rabbits have pink eyes and their fur is white except for the feet, tail, ears, and tip of the nose, which are black or dark brown (Fig. 62, center). When Himalayans are crossed with fully colored rabbits, the F_1 is colored, and in the F_2 there are three-fourths colored and one-fourth Himalayan. Himalayan albinism and color are, therefore, allelomorphs. It is interesting to see what happens when Himalayan is crossed with albino. If Himalayan and albino are due to different factors, each type should carry the allelomorph of the other; and reversion to full color should occur in F_1 as in the albino and black mice cited above (page 98). But the cross of Himalayan and albino rabbits produces *all Himalayan* in F_1 and three-fourths Himalayan and one-fourth albino in F_2. Reversion does not occur. Other experiments

show that the gene for Himalayan and the gene for albinism are never present together in the same gamete; a colored animal, for example, may carry *either* Himalayan *or* albino, but never

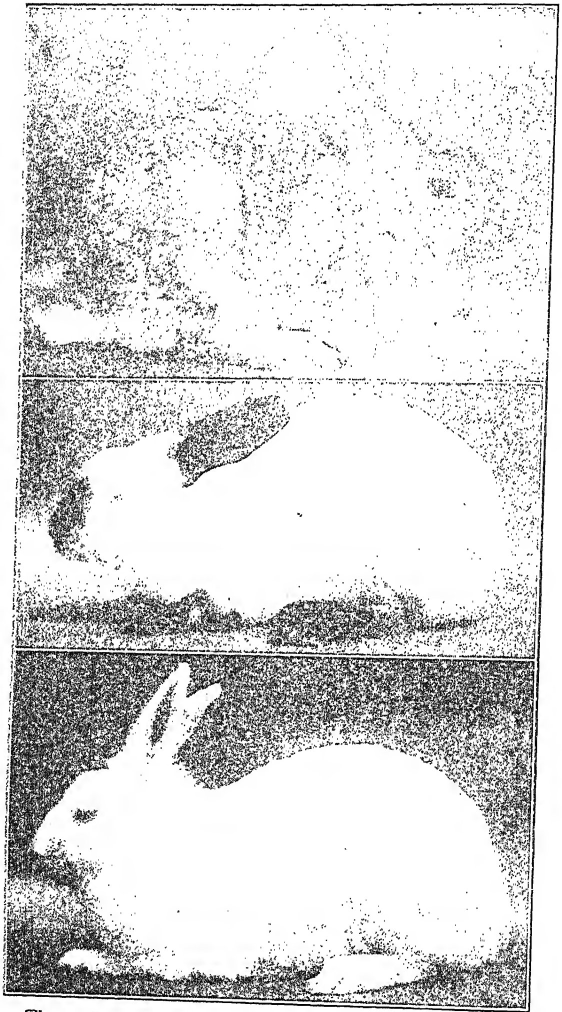


FIG. 62.—Three allelomorphs of a gene for coat color in rabbits. Top, colored; center, Himalayan albinism; bottom, complete albinism. (*From Castle, in Journal of Heredity.*)

both. It is evident then that Himalayan and albino are either allelomorphs or so closely linked that they never cross over to get into the same gamete. The evidence from the cross Hima-

layan × albino settles this point, since if these genes are not allelomorphs, each should have its own allelomorph, and the combination of these in F_1 should produce something different from either Himalayan or albino. It is believed, therefore, that these three conditions—color, Himalayan, and albinism—are all allelomorphic to each other; that is, they are determined at the same point in one pair of chromosomes. The members of such a system of three or more alternatives are known as *multiple allelomorphs.*

Many such series of allelomorphs are known. In rabbits there are four allelomorphs of the albino gene; in guinea pigs five members of an albino series are known; and in rats and mice there are three albino allelomorphs. In mice also the conditions of yellow, agouti, white-bellied agouti, and non-agouti coat color are allelomorphic. The largest series has been reported from *Drosophila* where the gene for white eyes has no less than ten allelomorphs. The occurrence of a number of alternative conditions of the same gene has supplied some very important information on the nature of genes, particularly with regard to their origin, and this matter will be referred to again in a later chapter. The significance of multiple allelomorphs at present lies in the evidence which they provide that allelomorphs, like linked factors, are located in the same pair of chromosomes, but unlike linked factors they never cross over and must be assumed to lie at the same point in homologous chromosomes.

The Widespread Occurrence of Linkage.—Linkage is not limited to the few examples which have been chosen for illustration. The history of mendelian inheritance and the history of linkage, the most important modification of mendelism, are in some respects parallel. Mendel's principles were established from careful breeding experiments with one plant, under the guidance of new methods and a new statistical notation. The application of these methods to other animals and plants produced results in essential agreement with those obtained by him. The principles of linkage were discovered during intensive breeding experiments with one animal, the fruit fly, under the guidance of Mendel's notation *plus* a new idea, the location of genes in the chromosomes.

Linked genes which behave like those in *Drosophila* and which probably admit of a similar interpretation have been found in many other animals and plants. In the corn plant, which

most nearly approaches *Drosophila* in the number of traits which have been studied, eight groups have been found, including about half of the fifty or more genes which have been identified. In the sweet pea, which furnished the original examples of linkage, Punnett has identified five groups of linked genes, accounting for twelve of the seventeen known genes in this plant; while among other plants linkage between at least two genes has been reported in the primrose, snapdragon, garden pea, tomato, bean, wheat, and others. Among animals, linkage has been discovered in the silkworm, grouse locust, pigeon, fowl, rat, mouse, rabbit, and others. The species in which it has been found are those which are most easily bred experimentally and in which the largest number of genes is known. Additional cases of linkage are being reported each year, and as knowledge of inheritance in these and other species increases, the number of genes known to be linked will doubtless be greatly augmented.

TABLE VII.—PERCENTAGE OF F_2 PHENOTYPIC CLASSES AS INFLUENCED BY VARIOUS DEGREES OF LINKAGE

Percentage of F_1 cross-over gametes	Percentage of F_2 zygotes when							
	A and *B* enter together (Cross of *AA BB* × *aa bb*)				*A* and *B* enter separately (Cross of *AA bb* × *aa BB*)			
	AB	*Ab*	*aB*	*ab*	*AB*	*Ab*	*aB*	*ab*
50.0[1]	56.2	18.7	18.7	6.2	56.2	18.7	18.7	6.2
33.3	61.1	13.9	13.9	11.1	52.8	22.2	22.2	2.8
25.0	64.1	10.9	10.9	14.1	51.6	23.4	23.4	1.6
20.0	66.0	9.0	9.0	16.0	51.0	24.0	24.0	1.0
16.6	67.4	7.6	7.6	17.4	50.7	24.3	24.3	0.7
14.3	68.4	6.6	6.6	18.4	50.5	24.5	24.5	0.5
12.5	69.1	5.9	5.9	19.1	50.4	24.6	24.6	0.4
11.1	69.7	5.2	5.2	19.7	50.3	24.7	24.7	0.3
10.0	70.3	4.7	4.7	20.3	50.2	24.8	24.8	0.2
1.0	74.5	0.5	0.5	24.5	50.0+	24.9	24.9	0.0+
0.0[2]	75.0	0.0	0.0	25.0	50.0	25.0	25.0	0.0

[1] No linkage, giving ordinary dihybrid ratio, 9:3:3:1.

[2] No crossing-over, giving 3:1 ratio; not distinguishable from case in which *A* and *B* are allelomorphs.

In the preceding paragraphs the assumption has been made that linked genes are located in the same pair of chromosomes. This assumption explains so well the many facts at hand that the student may be inclined to grant it unconsciously or for convenience. But there is other specific evidence of the agreement between the results of breeding experiments and the behavior of the chromosomes which has furnished a critical test of the chromosome theory, and has led to a recognition of its great value as a general explanation and description of the mechanism of heredity. This theory forms the subject of the next chapter.

QUESTIONS FOR THOUGHT AND DISCUSSION

78. How would you prove that purple flower color and dark stem color in *Datura*, which occur together, are due to a single gene rather than to two linked genes?

79. How would you determine whether characters which show no crossing-over were due to allelomorphs or to closely linked genes?

80. In *Drosophila* the gene for red, eosin, and white eye color are allelomorphs. The gene for yellow is linked with white eye with a cross-over value of 1.5 per cent. What is the probable cross-over value between eosin and yellow?

PROBLEMS

132. Assume that genes A and B are linked and show 40 per cent of crossing-over. If a homozygous individual (AB) (AB) is crossed with one which is $(ab)(ab)$, what will be the genotype of the F_1? What gametes will the F_1 produce, and in what proportions? If the F_1 is crossed back with a double recessive individual, what will be the appearance and genotypes of the offspring?

133. If the original cross is $(Ab)(Ab) \times (aB)(aB)$, what will be the genotype of the F_1? What gametes will it produce? If the F_1 is crossed back with a double recessive, what will be the appearance of the offspring?

134. What will be the appearance of the F_2 $(F_1 \times F_1)$ of the crosses described in the two preceding questions?

135. An individual homozygous for genes CD is crossed with one homozygous for cd and the F_1 crossed back to the double recessive. The appearance of the offspring is as follows:

903 CD
898 cd
98 Cd
102 cD

Explain this result, giving the crossover value between C and D. If assortment between C and D were independent, what would be the result of this cross?

136. If the cross in the preceding question had been between a homozygous Cd individual and a homozygous cD one, what would be the result of the cross of $F_1 \times$ the double recessive?

137. An individual homozygous for Ef is crossed with one homozygous for eF. The F_1 crossed back on a double recessive gives the following offspring:

762 Ef
758 eF
243 EF
237 ef

What would be the appearance of the F_2 from a cross of $(EF)(EF) \times (ef)(ef)$?

138. Calculate the percentage of crossing-over between the factors for colorless aleurone and shrunken endosperm in corn from the combined data from both coupling (page 154) and repulsion (page 156) experiments.

Note.—In *Drosophila* the mutant known as "black" (b) has a black body in contrast to the wild type, which has a gray body; and the mutant "arc" (a) has wings which are somewhat curved and bent downward, in contrast to the straight wings of the wild type.

139. In the two following crosses the parents are given (homozygous in each case) together with the counts of the offspring of F_1 females bred to black, arc males (data from Bridges and Morgan):

I. Black, arc $\times$ wild type (gray, straight)
F_1 females $\times$ black, arc males give:

Gray, straight	1,641
Gray, arc	1,251
Black, straight	1,180
Black, arc	1,532

II. Black, straight $\times$ gray, arc
F_1 females $\times$ black, arc males give:

Gray, straight	281
Gray, arc	335
Black, straight	335
Black, arc	239

From these data calculate the crossover value between black and arc.

Note.—In *Drosophila* the mutant known as "vestigial" (v) has wings which are very much reduced as compared with the long wings of the wild type.

140. In the two following crosses the parents are given, as in the previous question, together with the counts of offspring of F_1 females × black, vestigial males (data from Bridges and Morgan):

I. Black, vestigial × wild type (gray, long)
F_1 females × black, vestigial males give:

Gray, long	822
Gray, vestigial	130
Black, long	161
Black, vestigial	652

II. Black, long × gray, vestigial
F_1 females × black vestigial males give:

Gray, long	283
Gray, vestigial	1,294
Black, long	1,418
Black, vestigial	241

From these data calculate the crossover value between black and vestigial.

Note.—In rabbits, the "English" type of coat (white-spotted) is dominant over non-English (unspotted), and short hair is dominant over long hair (Angora).

141. When homozygous English, short-haired rabbits were crossed with non-English Angoras and the F_1 crossed back to non-English Angoras, the following offspring were obtained (data from Castle):

72 English, short-haired
69 non-English, Angora
11 English, Angora
3 non-English, short-haired

How closely linked are these genes for coat color and hair length?

Note.—In tomatoes Jones has found that tall vine is dominant over dwarf, and spherical fruit shape over pear. Vine height and fruit shape are linked, with a cross-over percentage of 20 per cent.

142. If a homozygous tall, pear-fruited tomato is crossed with a homozygous dwarf, spherical-fruited one, what will be the appearance of the F_1? of a cross of the F_1 with a dwarf, pear? of the F_2?

143. What *genotypically different* types will there be in the F_2 of the preceding cross? What offspring will each of these produce if selfed?

144. A certain tall, spherical-fruited tomato plant crossed with a dwarf, pear-fruited one produces 81 tall, spherical; 79 dwarf, pear; 22 tall, pear; and 17 dwarf, spherical. Another tall spherical plant crossed with a dwarf pear produces 21 tall, pear; 18 dwarf, spherical;

5 tall, spherical; and 4 dwarf, pear. What are the genotypes of these two tall, spherical plants? If they were crossed what would their offspring be?

145. In Chinese primroses, a cross between a plant homozygous for short style and magenta flower and one homozygous for long style and red flower gives an F_1 all of which is short-styled and magenta-flowered. This F_1 crossed with a long-styled, red-flowered plant gives the following offspring (data from Altenburg):

Short, magenta	1,697
Long, red	1,558
Short, red	195
Long, magenta	234

Calculate the linkage between style length and flower color

146. If the cross in the previous question had been between pure types of short red and long magenta, and the F_1 crossed with long red, what offspring would be expected?

Note.—The inheritance of grain color in wheat is described on page 108.

147. What would be the F_2 ratio of red and white grains from a cross of red by white, if two duplicate factors for red were linked, with a cross-over value of 10 per cent?

Note.—In rats, dark eyes are due to the interaction of two genes, R and P, the recessive allelomorph of either producing light-eyes. These genes are in the same chromosome.

148. When homozygous dark-eyed rats $(RP)(RP)$ were crossed with double recessive ones $(rp)(rp)$ and the F_1 crossed back with the double recessive, the following offspring were obtained (data from Castle):

Dark-eyed	1,255
Light-eyed	1,777

When $(Rp)(Rp)$ animals were crossed with $(rP)(rP)$ ones and the F_1 crossed back with the double recessive, the following offspring were obtained:

Dark-eyed	174
Light-eyed	1,540

Calculate the linkage between R and P.

149. If the dark-eyed rats obtained from the back-crosses in the two preceding questions were bred among themselves, what would their offspring be like?

150. Assume that genes A and B are linked, with a cross-over percentage of 20 per cent; and that C and D are also linked, with a cross-over

percentage of 10 per cent, but are in another chromosome. Cross a plant homozygous for *ABCD* with one which is *abcd* and cross the F_1 back on *abcd*. What will be the appearance of the offspring of this cross?

Note.—In garden peas, glaucous foliage (B) is dominant over green (b); free seeds (F) over adherent ones (f); rose flowers (R) over white ones (r); and late flowering (L) over early (l). Glaucous is linked with free, showing a cross-over of about 11 per cent, and rose is linked with late, showing a cross-over of about 12½ per cent and these two groups are in different chromosomes (data from White).

151. If a homozygous glaucous, free, rose, early pea plant is crossed with a homozygous green, adherent, white, late one, and the F_1 crossed back on a green, adherent, white, early, what will be the appearance of the offspring?

Note.—In tomatoes, red fruit color is dominant over yellow and is independent of the factors for height and fruit shape (for other data see question 142).

152. Cross a homozygous tall, spherical-fruited, red-fruited plant with a dwarf, pear-fruited, yellow-fruited one, and then cross the F_1 back with a dwarf, pear, yellow. What will be the appearance of the offspring?

Note.—In corn, sun-red plant color, R (see page 24) is dominant over normal green plant color, r, and is not linked with C or S.

153. Describe the probable appearance of an F_2 generation from a cross of a sun-red plant with colorless, full seeds by a green plant with colored, shrunken seeds (both parents homozygous).

154. In sweet peas, if a breeder crosses a homozygous, procumbent, hairy, white-flowered plant with a bush, glabrous, colored-flowered one, the F_1 is all procumbent, hairy, and colored-flowered. If this F_1 is crossed on a bush, glabrous, white-flowered plant, the offspring would be expected to show approximately the following distribution (data adapted from Punnett):

6 per cent procumbent, hairy, colored
19 per cent procumbent, hairy, white
6 per cent procumbent, glabrous, colored
19 per cent procumbent, glabrous, white
6 per cent bush, hairy, white
19 per cent bush, hairy, colored
6 per cent bush, glabrous, white
19 per cent bush, glabrous, colored

Explain these results, determining the strength of such linkages as may be observed.

155. Assume that an individual homozygous for XY is crossed with one homozygous for xy and that the F_2 from this cross is as follows:

$$334\ XY,\ 37\ Xy,\ 38\ xY,\ \text{and}\ 87\ xy.$$

How different is this result from what you would expect if assortment between X and Y were independent? What is the linkage between X and Y? (See Table VII, page 168 for calculating the percentage of crossing-over from F_2 ratios.)

156. Using the data given in your text for the F_2 of a cross in sweet peas between purple-flowered, long-pollened plants, and red-flowered, round-pollened ones, determine the strength of the linkage between flower color and pollen shape.

157. In sweet peas, a cross between a homozygous bright-flowered, tendril-leaved plant, and a dull-flowered, acacia-leaved (tendrilless) plant produced an F_1 which was all bright, tendril. The F_2 from this cross was as follows (data from Punnett):

424 bright, tendril
99 dull, tendril
102 bright, acacia
91 dull, acacia

The cross of bright, acacia on dull, tendril also gave an F_1 which was all bright, tendril, but the F_2 in this case was as follows:

847 bright, tendril
298 dull, tendril
300 bright, acacia
49 dull, acacia

Estimate from Table VII, the linkage between these two pairs of genes.

Note.—In mice the following genes which affect coat color form a series of multiple allelomorphs: yellow (A^Y); agouti (A^G) and non-agouti (a). A^YA^Y animals do not survive till birth (page 114).

158. What will be the appearance of the offspring of the following crosses?

$$A^YA^G\ Bb \times aa\ bb$$
$$A^Ya\ Bb \times A^GA^G\ Bb$$
$$A^Ya\ BB \times A^YA^G\ bb.$$

159. A yellow mouse from a race which throws nothing but yellows and agoutis is bred to a brown mouse. Cross their yellow and non-yellow offspring together. What will this F_2 look like?

160. Cross a yellow mouse from a race which throws nothing but yellows and blacks, with a pure agouti. What will be the appearance of the various possible F_2 populations?

161. Find the genotypes of the parents in the following crosses:

Yellow × brown giving one-half yellow, one-fourth agouti, one-fourth cinnamon.

Yellow × cinnamon giving one-half yellow, one-fourth agouti, one-fourth black.

Yellow × yellow giving two-thirds yellow, one-fourth agouti, one-twelfth cinnamon.

Note.—In mice there are two types of agouti, agouti with white belly (A^W) and agouti with gray belly (A^G). The former is dominant over the latter, and both are recessive to A^Y and dominant to a.

162. What will be the appearance of the offspring of the following crosses

$A^YA^W\ BB \times A^WA^G\ Bb$ $\qquad$ $A^Ya\ BB \times A^WA^G\ BB$

$A^YA^G\ bb \times A^WA^G\ BB$ $\qquad$ $A^YA^G\ BB \times A^Wa\ BB$

$A^Ya\ bb \times A^WA^G\ BB$ $\qquad$ $A^Wa\ bb \times A^Ga\ Bb$

$A^Ya\ Bb \times A^Wa\ Bb$

What are the genotypes of the parents in the two following crosses?

163. Yellow × white-bellied agouti giving one-half yellow, one-fourth white-bellied agouti, and one-fourth gray-bellied agouti. Give two genotypes which would produce this and tell how you would decide which was correct.

164. White-bellied agouti × gray-bellied agouti giving three-eighths white-bellied agouti, one-eighth white-bellied cinnamon, three-sixteenths gray-bellied agouti, one-sixteenth gray-bellied cinnamon, three-sixteenths black, one-sixteenth brown.

165. In corn there are several factors which affect plant color. Three of these are *sun-red, weak sun-red,* and *dilute sun-red,* their intensities being in the order named. Following are the results of crosses between these three types (data from Emerson): Sun-red × dilute sun-red gave all sun-red in F_1, and 998 sun-red to 314 dilute sun-red in F_2; weak sun-red × dilute sun-red gave all weak sun-red in F_1, and 1,300 weak sun-red to 429 dilute sun-red in F_2; sun-red × weak sun-red gave all sun-red in F_1, and 71 sun-red to 16 weak sun-red in F_2.

Explain these results, stating the relationship between these three plant colors.

166. In corn, normal leaf is dominant over liguleless leaf. If a homozygous sun-red, normal-leaved plant is crossed with a dilute, liguleless one, the F_1 is all sun-red, normal. This F_1, crossed back on dilute, liguleless, gave 104 sun-red normal; 99 dilute, liguleless; 41 dilute, normal; and 48 sun-red, liguleless. If a homozygous sun-red normal plant were crossed with a weak sun-red, liguleless, and the F_1 crossed back on a weak sun-red, liguleless, what offspring would you expect?

REFERENCE ASSIGNMENTS

49. Name at least two other ways, in addition to linkage, in which the association of two or more characters in inheritance might be explained.

50. Compare the "reduplication hypothesis" of Bateson and Punnett with the linkage hypothesis of Morgan. Which in your judgment is the better explanation of the facts?

51. What is the chiasma-type theory of crossing-over?

52. At what period during the development of the germ cells is it most probable that crossing-over takes place?

53. Describe the effect of at least one environmental factor on crossing-over in *Drosophila*.

54. Describe a series of multiple allelomorphs other than those described in detail in the text or problems.

55. What evidence is there for believing that characters which do not show crossing-over are due to allelomorphic rather than to closely linked genes?

56. Compile a list of cases of linkage in five animal and five plant species, giving the strength of linkage in each case. Do not include cases given in detail in text or problems.

CHAPTER VIII

THE CHROMOSOME THEORY OF INHERITANCE

The facts presented in the preceding chapter have led to the conclusion that linkage, instead of being a sporadic exception to mendelian inheritance, is actually a widespread, orderly occurrence, subject to laws which are not only of the same cogency as those dealing with the segregation of unit factors, but which also give a reasonable explanation of the *mechanism* of segregation and assortment. The facts of linkage are best explained by assuming that linked characters are located in the same chromosome, and that breaks in the linkage, or cross-overs, are due to an actual interchange of parts between homologous chromosomes.

Such conclusions have been amplified by further research into a general theory, the chromosome theory of inheritance, which maintains that all of the factors of the organism are located in the chromosomes. This is a very broad statement, with many suggestive implications. It means for one thing that the genes are actual particles of living material, occupying a measurable portion of space, and that many hundreds of them must be packed away in the small compass of a tiny thread of chromatin which can only be seen with the highest powers of the microscope. The nucleus of each cell is on this view to be regarded as a complex aggregation of units which are arranged and guided through the processes of inheritance and development by those laws which in the end are the physical and chemical laws of living matter. Thus a whole new field of knowledge has been opened up, and a large number of investigators are now trying to discover the specific laws which govern the behavior of the genes in the chromosomes.

The Genes of Drosophila.—Up to the present most of the evidence on linkage and the chromosome theory has been derived from one animal, the fruit fly, *Drosophila*. This species has for fifteen years been carefully studied both by geneticists and cytologists and has proved to be the best material yet found for breeding experiments. It breeds readily in captivity and is

extremely prolific, a single pair of flies producing upwards of two hundred progeny within three weeks after mating. Its chief advantage for genetic studies, however, is its great variability, for the wild-type fly has produced spontaneously under

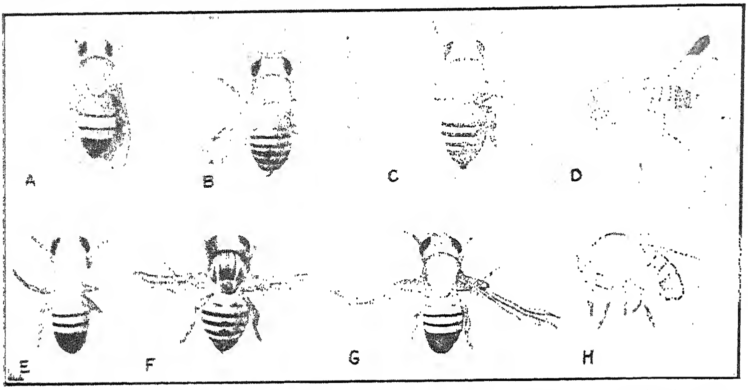


FIG. 63.—Some of the variations, chiefly affecting the wings, which have arisen by mutation in *Drosophila*. *A*, "truncate," *B*, "balloon," *C*, "vestigial," *D*, "jaunty," *E*, "apterous," *F*, "strap," *G*, "antlered," *H*, "dachs." (*After Bridges and Morgan.*)

domestication hundreds of sports or mutations, which have given rise to true-breeding varieties. Many of these variations are well marked and easily distinguished with or without the microscope. Examples of some of the mutant types are shown

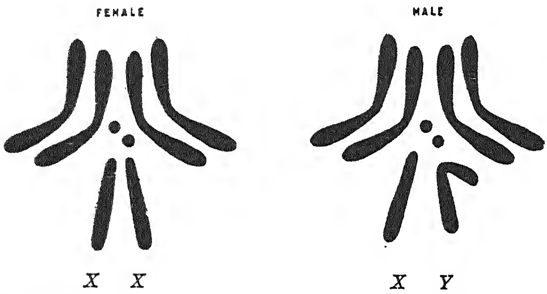


FIG. 64.—Diagram showing the four pairs of chromosomes in *Drosophila*. *X and Y designate the sex chromosomes.* (*After Bridges.*)

in Fig. 63. The inheritance of over two hundred distinct characters of this sort has been traced to genes which are inherited according to the mendelian principle of segregation.

It has been discovered that the characters of *Drosophila* occur in four groups (Table VIII), the genes in each group being linked

TABLE VIII.—PARTIAL LIST OF THE FOUR GROUPS OF LINKED TRAITS IN DROSOPHILA

Group I	Group II	Group III	Group IV
(*Sex-linked*)	abrupt	[illegible]	bent
abnormal	amethyst	[illegible]	eyeless
bar	antlered	[illegible]	shaven
bifid	apterous	[illegible]	
blood	arc	bithorax	
bordered	aristaless	cardinal	
broad	balloon	claret	
buff	black	cream-III	
cherry	blistered	compressed	
cleft	brown	curled	
club	chubby	deformed	
crooked	cinnabar	delta	
cross-veinless	confluent	dichaete	
cut	cream II	dilute	
depressed	curly	divergent	
double	curved	dwarf	
dusky	dachs	ebony	
echinus	dachsoid	extended	
ecru	dachsous	giant	
eosin	dash	glass	
facet	detached	hairless	
forked	expanded	hairy	
furrowed	flipper	intensifier	
fused	fringed	kidney	
garnet	gap-vein	lethals (9)	
ivory	gull	mahogany	
lemon	humpy	maroon	
lethals (50)	jaunty	minute	
lozenge	lethals (9)	olive-III	
miniature	lobe	pale-III	
notch	minute	peach	
prune	morula	pink	
roughish	narrow	pointed-wing	
ruby	nick	roof	
rudimentary	oblique	rotated	
sable	olive	rough	
scute	pads	roughoid	
short	pale-II	safranin	
singed	patched	scarlet	
small-eye	pinkish	sepia	
small-wing	pink-wing	ski-III	
spot	purple	smudge	
tan	purploid	sooty	
tiny bristle	reduced	spineless	
tinged	roof	spread	
vermilion	safranin	tilt	
white	scraggly	tumor	
yellow	ski-II	two-bristles	
	sienna	varnished	
	snub	vortex-III	
	square	warped	
	speck	white-ocelli	
	star	with	
	strap		
	straw		
	streak		
	telegraph		
	telescope		
	translucent		
	trefoil		
	truncate		
	vortex		
	yellowish		

with one another but inherited independently of those in every other group. It is also known that there are four pairs of chromosomes in *Drosophila* (Fig. 64). One large chromosome has been found to be involved in the determination of sex, and one large group of genes is inherited in a peculiar *sex-linked* fashion as explained in Chap. IX. There are two other large groups of genes and two other large chromosomes; while only

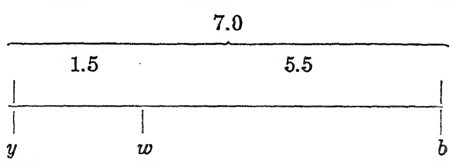
a few genes belonging to the fourth group have been found and the fourth chromosome is very small, being only about one-twelfth the size of the large ones. The correspondence between the groups of genes and the chromosomes, when considered together with the other evidence, is obvious. *There are as many groups of linked genes as chromosomes*, and each group represents the genes which are located in one chromosome. Morgan has called this the "principle of limitation of the linkage groups" and has assumed that in animals and plants generally the number of groups of linked genes is limited by the number of pairs of chromosomes. The evidence from *Drosophila* on this point is conclusive. No other animals or plants have been as thoroughly studied as this small fly, but wherever good evidence on both linkage and chromosomes is at hand, this principle holds good. Thus in peas there are seven pairs of chromosomes, and at least one representative of each of seven groups of genes is known.

Evidence such as the above, while cogent, is of a negative character, since it indicates only that the number of linkage groups has not been found to exceed the number of chromosome pairs. Evidence of a more positive sort has been provided by the combined results of genetic and cytological research with *Drosophila*. Bridges noted irregularities in the transmission of a gene which has been assigned to one of the four chromosomes of *Drosophila*. Cytological examination showed that in such cases this chromosome was transmitted in the same abnormal manner as the gene it was supposed to contain. This abnormal behavior, known as *non-disjunction*, is described in Chap. IX.

Arrangement of Genes in the Chromosome.—Breeding experiments with *Drosophila* have not only established the prime fact that the genes are located in the chromosomes, but they have also accomplished the more difficult feat of showing *how* they are *arranged* in the chromosomes. It has been shown that genes in the same linkage group (and thus presumably in the same chromosome) differ markedly in the strength with which they are linked. Now if it is assumed that the genes are distributed in a *single line* along the chromosome and that, in general, *the distance between two genes in a chromosome is proportional to the amount of crossing-over between them*, there is a basis for constructing a gene map of each chromosome for which there are sufficient data, and for actually locating the genes in a definite position in the chromatin. These two assumptions (with some qualifications

to be discussed later) have been tested by experiment and are now generally accepted as true.

If two genes A and B, for example, cross over very infrequently (say, in 5 per cent of the cases) they are assumed to be very *near* to each other on the chromosome, so that the chance that a break in the chromosome will occur in the short distance between them is very small. On the other hand, if two genes A and C appear to be very loosely linked and show crossing-over in a large percentage of the cases (say, in 35 per cent), they are assumed to lie relatively *far* apart on the chromosome since the chance of a break occurring within the long distance which separates them is relatively large. These assumptions are illustrated in Fig. 65. If they are true, then by measuring the amount of crossing-over between A and B, and, independently, between B and C, it should be possible to predict the amount of crossing-over between A and C, for if the linked genes *are on the same line,* and the amount of crossing-over between genes is proportional to the distance between them, then the distance AB plus the distance BC should equal the distance AC. In many cases this relationship is found to hold true. Thus in crosses between red-eyed, yellow-bodied and white-eyed, gray-bodied flies it has been found that crossing-over between yellow and white occurs in only about 1.5 per cent of the cases. In other crosses between white-eyed, normal-winged flies and red-eyed bifid-winged flies, crossing-over between white and bifid occurs in about 5.5 per cent of the cases. It may be assumed, then, that yellow and white are about 1.5 units[1] apart, while white and bifid are 5.5 units apart. If the gene for white lies on a line with and between the genes for yellow and bifid, one would expect to find that yellow-white (1.5) plus white-bifid (5.5) = yellow-bifid (7.0). Such is the case, for in independent experiments yellow and bifid show about 7 per cent of crossing-over. These three genes might be placed on a map which would show accurately the relations of the three genes as follows:



[1] The unit used for stating the distances which separate genes is that within which 1 per cent of crossing-over takes place.

This relation does hold with genes which display relatively little crossing-over and which are probably near together in the chromosome. It does not hold, however, with genes which are relatively far apart, so that the statement that the distance between genes is proportional to the amount of crossing-over between them must be qualified by specifying that the genes must be near together.

Double Crossing-over.—In many experiments with genes which show much crossing-over, it has been found that the amount of crossing-over appears to be lessened and the apparent distance between the distant genes appears to be shortened by the occurrence of *double crossing-over* or a break in two parts of the chromosome at once. Thus if three genes A, B, and C are located in one chromosome, crossing-over might take place between A and B and between B and C at the same time. If the cross $Aa\ Bb\ Cc \times aa\ bb\ cc$ were made, the following types of gametes formed by the heterozygote might be found.

Non-cross-overs	(ABC) (abc)	factors in their original combinations
Single cross-overs	(A-bc) (a-BC)	a break between A and B
	(AB-c) (ab-C)	a break between B and C
Double cross-overs	(A-b-C) (a-B-c)	breaks between A and B and between B and C at once.

The zygotes formed by the last two types of gametes resemble in one respect the non-cross-over type, since the parental combinations of factors AC and ac have been reconstituted by double crossing-over, so that in these gametes A and C have the same relation as in the parents. If these were the only two factors involved in such a case, these AC and ac combinations from the double cross-overs would be indistinguishable from the non-cross-over classes (AC and ac) and would be added to them, so that the percentage of crossing-over would seem to be less than the actual distance of A-C as determined by adding the distances AB and BC. The diagram in Fig. 65 and the legend accompanying it show the assumed chromosome mechanism of double crossing-over.

The hypothesis of double crossing-over explains those experimental results which are at variance with the theoretical expecta-

tion based on simple crossing-over. Thus when red-eyed, long-winged flies are crossed with white-eyed, miniature-winged

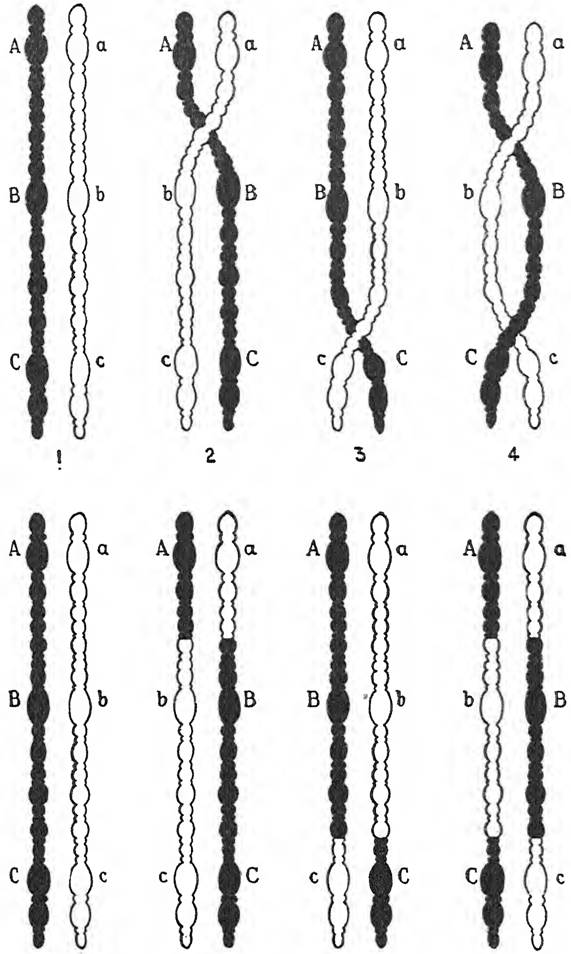


FIG. 65.—Diagram showing the mechanism (upper row) and the results (lower row) of crossing over in a pair of homologous chromosomes. (1) no crossing over; (2) crossing over between *A* and *B*; (3) crossing over between *B* and *C*, and (4) double crossing over between *A* and *B* and between *B* and *C*. The lower row shows the resulting chromosomes which pass into the gametes.

flies, it is found that crossing-over takes place between white and miniature in about 33 per cent of the cases. These genes are hence inferred to be about 33 units apart. Miniature and

bar (a gene which affects the shape of the eye) show about 22 per cent of crossing-over. The sum of these distances is 55, which, if no double crossing-over takes place, should represent the distance between white and bar. But in actual crosses of white and bar, the observed percentage of cross-overs is only 44. The reduction of the amount is assumed to be due to double crossing-over in the long distance between white and bar.

In arriving at the true distance between the genes in a chromosome, then, it is necessary to measure the long distances by adding together the sums of the shorter distances involved, since the shorter distances are not affected by double crossing-over. Thus to determine the true distance from *A* to *F*, it is necessary to measure, if possible, and add together the shorter distances *AB*, *BC*, *CD*, *DE*, and *EF*.

Interference.—A further complication has been discovered in the *Drosophila* experiments. This is the important fact that crossing-over in one region of a chromosome appears to interfere with or prevent crossing-over in an adjacent region. Thus, if two genes *A* and *B* appear to be about ten units apart, and *B* and *C* to be about ten units apart, whenever a cross-over occurs between *A* and *B*, the amount of crossing-over between *B* and *C* is greatly reduced. This might be explained on mechanical grounds by assuming that at synapsis, the chromosomes do not coil tightly about one another but are more or less rigid, so that if bent or coiled between *A* and *B*, they will be less liable to bend and cross again between *B* and *C*. It has been found that interference is not uniform throughout the length of the chromosome, but that it decreases up to a certain distance and disappears and then reappears beyond that point, as if the chromosome were so constructed that it was pliable in certain regions and rigid in others. It is probable that when double crossing-over occurs, the position of the two breaks in a chromosome is always separated by a minimum distance, which is the distance, for that particular chromosome and region, within which no breaking will take place.

These are the secondary or supporting principles of the chromosome theory:

1. The number of linkage groups is limited by the number of pairs of chromosomes of the organism.

2. The genes in each chromosome are arranged in a *single straight line*, and their distances apart are proportional to the amount of crossing-over between them.

And the chief complications are:

1. That crossing-over may take place in two widely separated regions of a chromosome at one time, tending to make distant genes appear to be nearer together.

2. That crossing-over in one region of a chromosome tends to prevent it in the adjacent regions and thus to reduce the amount of crossing-over between genes which are near the area involved in a single crossing-over.

For present purposes, no further complications need be considered although many have been met and solved. Consideration may now be given to the most spectacular achievement of recent genetic research, the mapping of the genes in the chromosomes of *Drosophila*.

Chromosome Maps.—In Fig. 66 are shown the most recent chromosome maps prepared for *Drosophila*. Each of the genes listed on the maps has been traced to one of the four chromosomes, by testing its linkage relations with each of the four groups. It has been located on the map by measuring its cross-over value with the genes which appeared to be nearest to it (assuming that 1 per cent of crossing-over equals one unit of distance) and then applying the necessary corrections for double crossing-over, interference, and other special conditions in the chromosome or region which is being mapped. It will be asked how distances in excess of 50 units can be possible, since crossing-over may vary only from nearly zero (no crossing-over) to nearly 50 per cent (independent assortment). It is true that the *amount of crossing-over* between two genes never exceeds 50 per cent, but, because of double crossing-over, it is necessary to measure long distances by adding together the sums of the cross-over values for intermediate genes as explained above. These sums frequently exceed 50 in the long chromosomes. In the second chromosomes, for instance, the genes for "star" and "speck" appear on the map as 105 units apart. When "star" and "speck" are crossed, they show less than 50 per cent of crossing over (actually about 48.7 per cent), but this is known to be due to the reduction caused by double crossing-over. When the intermediate percentages are added, the sum is in excess of 100, which expresses the true distance between these two genes.

"Map distance," therefore, does not always correspond to cross-over percentages as measured directly, and consequently the amount of crossing-over between two genes cannot be read

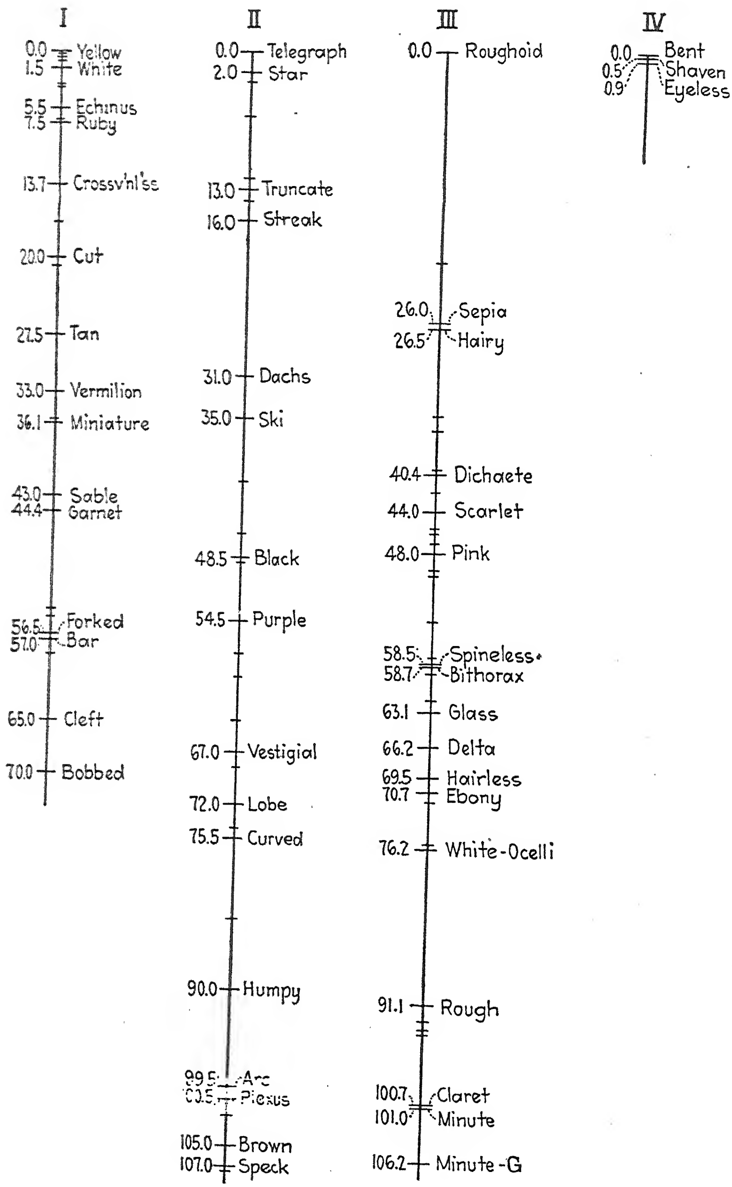


FIG. 66.—Maps of the four chromosomes of Drosophila, showing the position of the more important genes which have been located. Figures refer to distances from the end of the chromosome, as determined by percentage of crossing over. Chromosome I is the X chromosome. In chromosome II it has recently been found that the position of *star* is at o with *telegraph* 1.2 units below it. Each locus number in this chromosome as shown is thus approximately two units too large. (*After Morgan, Bridges and Sturtevant*, 1925.)

directly from the maps, except with genes so near together that no double crossing-over occurs in the distances between them. Several methods of converting "map distance" to cross-over percentages have been proposed. The student should be familiar with a method of this sort, chiefly because of the insight it gives into the technique of locating genes, and the knowledge of the chromosome theory which the calculations require. He should be warned, however, that the results of such conversion cannot be expected to be entirely accurate, nor to be exactly verified in any experiment which he might undertake. In any such method the units of measurement of the chromosome must be regarded as constant throughout each chromosome and for all the chromosomes, but there is good evidence that in *Drosophila* the different chromosomes, and different regions of the same chromosome, are inherently different and subject to different special conditions all of which are not yet known. A relation between cross-over percentage and map distance which holds good for one group of genes will not necessarily hold good for others, although when all of the possible variations in linkage have been studied, an exact method of conversion should ultimately be discovered.

The impossibility of expressing accurately the whole of inheritance in one simple formula illustrates well the fundamental complexity of the facts. The apparent confidence with which the mechanism of inheritance has been discussed, and the use of mathematical and mechanical symbols should not lead to the belief that the whole problem of inheritance is solved, nor that facility in dealing with the problems involved implies an understanding of the whole process. The chief gain from a discovery of the principle of linkage is that it is now possible to reduce to order and predictability a group of facts which for a long time were confusing and unexplained. This still further increases confidence in the belief that inheritance, once considered so capricious and puzzling a process, does conform to laws which, although complex, are similar to those of the physical sciences, and that with fuller knowledge these laws may be made the basis for the prediction and the control of heredity.

Significance of the Chromosome Theory.—The questions may now justly be asked: To what new knowledge of the mechanism of inheritance and of the nature of living things does the chromosome theory of inheritance lead? Of what significance is it in

science and in practice? Any scientific theory must finally be judged by its fruitfulness, and on this criterion the idea that the genes are located in the chromosomes has abundantly justified itself, for under its guidance more new and exact facts about inheritance have been discovered than in all the years before its employment. Among these facts are some fundamental conceptions as to the character of protoplasm, and particularly as to the nature and origin of the genes. Since the work of Mendel it has been known that the animal or plant may be viewed as an aggregation of separate units, which during the process of reproduction are passed on to the progeny in accordance with a few simple laws. From the work of Morgan and other investigators it is now known that the gene is a definite part of the chromosome with a definite location therein; and that it may exist in two or more alternative forms (allelomorphs), each of which produces some visible effect in one or more parts of the organism Within the space occupied by the gene, chemical or physical changes may take place which result in alternations in its expression. These changes are known as sports or gene mutations and they give rise to new characters as discussed in Chap. XI.

As an example of the kind of results to be expected from studies guided by the chromosome theory may be mentioned the possibility of determining the size of these ultimate units of living material. If the number of genes in a chromosome can be known or estimated and the bulk of the chromosome can be measured, then dividing this bulk by the number of genes in it will give an estimate of the size of a single gene. Morgan estimates that there are about 4,000 genes in *Drosophila*, and by the above and other methods, calculates that the mass of the gene is probably somewhat larger than the mass of some protein molecules which have been measured.

Indeed, now that genetic factors have been located at definite points in the living substance of the nucleus, it may become possible not only to estimate their size but to determine their chemical constitution and physical character, to learn how they affect development, and even to alter them at will, and thus to control inheritance. These new fields which the chromosome hypothesis has opened to the geneticist and the clearer picture which it has given him of the mechanism of heredity have made its development the most notable event in modern genetic investigation.

QUESTIONS FOR THOUGHT AND DISCUSSION

81. If four factors are found to assort independently in *Drosophila*, what must be their distribution in the chromosomes?

82. On the chromosome theory what explanation could be offered for the occurrence of five groups of linked factors in a species with four pairs of chromosomes?

83. From the data on chromosome numbers in the species of *Drosophila* (Chap. VI, Question 74) what differences in the linkage relations of the genes would you expect to find between species with eight and with ten or twelve chromosomes?

84. Are the chances of noting cases of linkage between characters greater or less in a species with forty chromosomes than in one with ten chromosomes? Explain.

85. Two genes (pink eye and albinism) are linked with about the same strength, in rats and mice, but in guinea pigs two similar genes are probably not linked. Guinea pigs have more chromosomes than rats or mice. What relationship may these facts have to each other?

86. What similarities in linkage and crossing-over would you expect to find between bees and *Drosophila* (see Chap. VI, Problem 130)? Explain.

87. Most lethal factors are not associated (as is yellow in mice) with a readily visible character, but each is, nevertheless, due to a gene in a definite locus in the chromosome. How would you determine the existence of such a lethal factor, and how would you find its linkage relations with other factors?

PROBLEMS

167. Assume that genes A, B, and C are in the same chromosome and occur in the order named; and that there is 40 per cent crossing-over between A and B and 10 per cent between B and C. An individual homozygous for ABC is crossed with one homozygous for abc. What gametes will the F_1 produce? If the F_1 is crossed back on abc, what will be the appearance of the offspring? Which individuals are the double cross-overs?

168. If a homozygous AC individual is crossed on ac and the F_1 crossed back on ac, what will be their offspring? Explain the difference between the cross-over percentage which is thus actually obtained with that which is obtained by adding together the percentages between A-B and B-C.

Note.—In calculating the cross-over value between two points when the cross-over values of two component distances are known, determine the number of double cross-overs by multiplying one percentage by the

other; multiply this value by two, and subtract this from the combined values for the two distances. Thus in Problem 167, there will be 10 × 40 per cent of double cross-overs, or 4 per cent; the distance between A and C is 40 plus 10 units, or 50 units, which minus 8, or 2 × 4, or is 42, the true cross-over value of A and C.

169. Cross a homozygous AbC individual with one that is homozygous for aBc. What gametes will the F_1 produce? If the F_1 is crossed back on abc, what will be the appearance of the offspring?

170. Assume that genes D, E, and F are in the same chromosome, and arranged in that order, and that there is 8 per cent crossing-over between D and E and 25 per cent between E and F. What will be the cross-over value between D and F?

171. In corn, colorless aleurone (c) is recessive to colored (C); shrunken endosperm (s) is recessive to full (S), and waxy endosperm (w) is recessive to starchy (W). Factors c and s are closely linked (see page 154). A cross of colored starchy × colorless waxy produced all colored starchy seeds in F_1. The F_1 was back-crossed to colorless waxy, and the following progeny produced (data from Hutchison):

Colored, Starchy	Colored, Waxy	Colorless, Starchy	Colorless, Waxy
2,542	717	739	2,710

(*a*) Is there any linkage between C and W?
(*b*) If so what is the cross-over value?
(*c*) On the basis of this result would you expect the factors S and W to be linked or independent?

172. F_1 plants from the cross of shrunken starchy corn × full waxy were back-crossed to shrunken waxy. The results are given below:

Full, Starchy	Full, Waxy	Shrunken, Starchy	Shrunken, Waxy
1,531	5,991	5,885	1,488

What linkage, if any, exists between shrunken and waxy?

173. In corn, F_1 plants from the cross of colored, shrunken, starchy × colorless, full, waxy were crossed with colorless, shrunken, waxy plants, and the following progeny observed (data from Hutchison):

Colored, shrunken, starchy	2,538
Colorless, full, waxy	2,708
Colored, full, waxy	116
Colorless, shrunken, starchy	113
Colored, shrunken, waxy	601
Colorless, full, starchy	626
Colored, full, starchy	4
Colorless, shrunken, waxy	2

On the basis of these and two preceding counts, map the positions of *C*, *S*, and *W* in the chromosome.

174. Assume that *G*, *H*, and *I* are in the same chromosome and known to be arranged in that order. Between *G* and *H* there is 30 per cent crossing-over and between *H* and *I*, 20 per cent. If homozygous *Gi* is crossed on homozygous *gI* and the F_1 crossed back on *gi*, what will be the appearance of the offspring?

175. Genes *J*, *K*, and *L* are in the same chromosome and occur in that order. The F_1 of the cross $JK \times jk$, crossed back on *jk*, gives 349 *JK*, 350 *jk*, 151 *Jk*, and 148 *jK*.

The F_1 of the cross $KL \times kl$, crossed back on *kl*, gives 212 *KL*, 213 *kl*, 36 *Kl*, and 38 *kL*.

If *Jl* is crossed with *jL* and the F_1 crossed back on *jl*, what will be the appearance of the offspring?

Map the chromosome in which these genes occur.

176. In Chinese primroses short style is dominant over long, magenta flower over red, and green stigma over red. When from the cross of homozygous short, magenta flower, green stigma on long, red flower, red stigma, the F_1 was crossed back on long, red flower, red stigma, the following offspring were obtained (data from Altenburg):

Style	Flower	Stigma	
Short	Magenta	Green	1,063
Long	Red	Red	1,032
Short	Magenta	Red	634
Long	Red	Green	526
Short	Red	Red	156
Long	Magenta	Green	180
Short	Red	Green	39
Long	Magenta	Red	54

Map the chromosome in which these genes lie.

177. In the Chinese primrose, if a plant homozygous for long style, red flowers, and green stigmas is crossed with one homozygous for short style, magenta flowers, and red stigmas, and the F_1 is crossed with a triple recessive, what will be the appearance of the offspring?

178. In *Drosophila*, red eyes, large normal wings, and straight spines are dominant over white eyes, miniature wings, and forked spines. In a cross between a homozygous red, large, straight and a white, miniature, forked, the F_1 female, back-crossed on a white, miniature, forked male, gave the following. (See Table at top of p. 192.)

White miniature, forked	26.8 per cent
Red, large, straight	26.8 per cent
White, large, straight	13.2 per cent
Red, miniature, forked	13.2 per cent
White, miniature, straight	6.7 per cent
Red, large forked	6.7 per cent
White, large, forked	3.3 per cent
Red, miniature, straight	3.3 per cent

Explain these results and map the chromosome, giving distances between the genes.

179. In *Drosophila* the mutant "morula" (m) has a peculiar eye modification in which the facets are more irregular in size, shape, and color than are those of the normal eye. For descriptions of mutants "black" and "arc," see Problem 139.

In the four following crosses the genes for black, arc, and morula entered the crosses in all four possible combinations, as stated. The counts in each case are the results of mating F_1 females with black, arc, morula males. Only the recessive allelomorphs are named, the normal dominant allelomorphs being assumed to be present unless the recessive is mentioned. Thus "black" flies are bAM, possessing the dominant allelomorphs of arc and morula. The four crosses are as follows:

I. Black, arc, morula × wild type; F_1 female × black, arc, morula male.
II. Black, arc, × morula; F_1 female × black, arc, morula male.
III. Black, morula × arc; F_1 female × black, arc, morula male.
IV. Black × arc, morula; F_1 female × black, arc, morula male.

The results of these four back crosses are given below (data from Bridges and Morgan):

	Cross I	Cross II	Cross III	Cross IV
Wild type	613	95	3	164
Black	445	40	13	187
Arc	38	713	113	21
Morula	82	851	107	7
Black, arc	55	884	96	8
Black, morula	29	666	120	15
Arc, morula	467	33	14	187
Black, arc, morula	514	79	2	133

Determine the cross-over value between black and arc, arc and morula, and black and morula. Map the chromosome for these three points.

180. Determine the total number of double cross-overs in the previous problem and compare it with what would theoretically be expected through the independent operation of the two single cross-overs. How do you explain this difference?

181. Below are the data from Bridges and Morgan for the cross-overs between the genes black, curved, purple, speck, star, and vestigial in chromosome II of *Drosophila.* On the basis of the data, map the chromosome for these five genes as accurately as possible. Remember that determinations for short distances are more accurate than those for long ones.

Genes	Total flies	Cross-overs
Black-curved	62,679	14,237
Black-purple	48,931	3,026
Black-speck	685	326
Black-star	16,507	6,250
Black-vestigial	20,153	3,578
Curved-purple	51,136	10,205
Curved-speck	10,042	3,037
Curved-star	19,870	9,123
Curved-vestigial	1,720	141
Purple-speck	11,985	5,474
Purple-star	8,155	3,561
Purple-vestigial	13,601	1,609
Speck-star	7,135	3,448
Speck-vestigial	2,054	738
Star-vestigial	450	195

Locate also on this map the genes for arc and morula, studied in problem 179. (Arc and morula are on the opposite side of black from star.)

182. A breeder of Chinese primroses has three plants, each of which has short styles, magenta flowers, and green stigmas. The offspring of each, when crossed on a triple recessive plant, are presented below, symbols being used instead of words (*L* short style, *l* long, *R* magenta flower, *r* red, *S* green stigma, *s* red).

Plant 1 × *lrs*	Plant 2 × *lrs*	Plant 3 × *lrs*
290 *LRs* 151 *LRS* 288 *lrS* 147 *lrs* 37 *LrS* 20 *Lrs* 39 *lRs* 21 *lRS*	40 *LRs* 19 *LRS* 37 *lrS* 21 *lrs* 289 *LrS* 150 *Lrs* 291 *lRs* 148 *lRS*	221 *LRS* 218 *lrS* 57 *LrS* 60 *lRS*

What are the genotypes of these three plants?

183. Genes *A* and *B* are in one chromosome, with a cross-over of 20 per cent; *C*, *D*, and *E* are in another chromosome and arranged in that order. Between *C* and *D* is a cross-over value of 10 per cent, and between *D* and *E*, one of 15 per cent. *F* and *G* are in another chromosome, with a cross-over value of 30 per cent. *H* is in another chromosome. Cross a homozygous *ABCDEFGH* individual with an *abcdefgh* one, and cross the F_1 back on *abcdefgh*. What will be the chances of getting individuals of the following phenotypes:

ABCDEFGH
ABCDeFgh
AbCdEfgH

184. In chromosome II of *Drosophila* (data from Bridges and Morgan) occurs the gene for "curved" wings (*c*), the dominant allelomorph of which (*C*) produces normal long wings. In this chromosome occurs a lethal factor *l*, which when homozygous causes the death of the individual. *LL* and *Ll* animals live, *ll* ones die. The gene for "curved" shows a cross-over value of 8.7 per cent with this lethal gene. Cross two flies of the genotype (*CL*)(*cl*) together; cross two others of the genotype (*Cl*)(*cL*). What will be the appearance of the offspring in each case?

185. Assume that *A* and *B* are the genes for two visible characters and *l* a lethal; that all three are linked; and that they occur in the order *ALB*. Assume that there is a cross-over of 20 per cent between *A* and *L*, and of 10 per cent between *L* and *B*. Cross two individuals which are (*ALB*)(*alb*). What will be the appearance of the offspring?

186. In rats two genes *r* and *p* (referred to in Problem 148) are linked. *RR pp* animals have pink eyes and light-colored coats; *rr PP* animals have red eyes and light-colored coats. *RR PP* animals have dark eyes and dark coats. Albinism, *cc* (pink eyes and white coat), is also linked with *r* and *p*. Design an experiment to measure this linkage and to map the chromosome containing *r*, *p*, and *c*, giving all necessary steps and crosses.

REFERENCE ASSIGNMENTS

57. What evidence for the "limitation of the linkage groups" is there from organisms other than *Drosophila?*

58. What methods have been proposed for converting "map distance" into cross-over percentages and *vice versa?*

59. What kind of evidence would be required to show that the genes are not arranged in a single straight line in the chromosomes?

60. Look up and describe a case of "deficiency" in *Drosophila.* Do such cases strengthen or weaken the chromosome theory? Why?

61. What is meant by "balanced lethal" factors and how do they explain the occurrence of hybrids that breed true?

CHAPTER IX

SEX AND ITS INHERITANCE

In all animals and plants except the very lowest, sexual reproduction involves the union of two gametes which are markedly different from one another. One of them is relatively small and ordinarily motile and is known as the *male* gamete, and the other is relatively large and inactive and known as the *female*. Among plants both types of sexual cells are usually produced by every

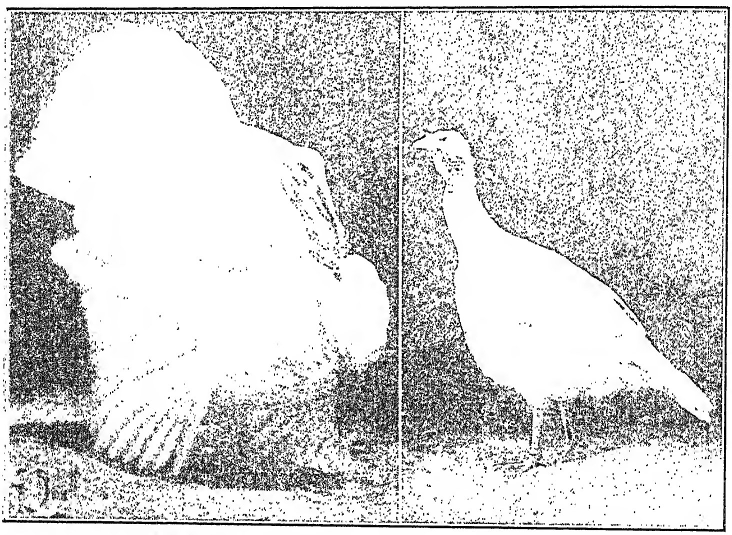


FIG. 67.—Sexual differences in birds as shown in turkeys—male at left, female at right. (*From Robinson.*)

individual, which is thus truly bisexual or hermaphrodite; but in the case of most animal species a given individual will produce either male gametes or female ones, but not both, so that a sharp distinction appears between two types of sexually different forms, males and females, within the same species (Fig. 67). Furthermore, sexual reproduction, as one of the major functions of the higher animals and plants, requires not only specialized sexual

structures themselves but the coördination of all the parts, activities, and instincts of the individual, and the development of specific secondary structures and functions which aid in the successful union of the sexual cells. The fundamental sexual differences are, therefore, usually accompanied by a marked diversity in size, general metabolism, instincts, and structures involved in mating or fertilization; and in such characters in animals as combs, horns, hair, and plumage, the development of which is influenced by the presence of the sexual glands.

The distinction between a male and a female is thus usually far more profound than that between two individuals differing in one of the comparatively minor traits which, because of ease of observation, have been the subject of breeding experiments. The inheritance of sex and its accompanying characters is of great importance in genetic theory and presents a number of problems which are quite distinct from those involved in the heredity of other traits. These problems concern primarily the members of the animal kingdom, for in the great majority of plants there is no distinction between male and female individuals.

The Problem.—The chief problem is to explain the distribution and inheritance of the primary sexual differences themselves. What determines that one individual will be a male and produce sperm, while another develops as a female and produces eggs? These two kinds of individuals among the higher animals are usually produced in approximately equal numbers, although there are many exceptions to this rule. It is also true that the differences between the sexes are usually quite distinct and discontinuous, so that there is ordinarily no difficulty in classifying every individual as definitely male or definitely female. These facts suggest the operation of some exact mechanism governing the production of the two sexes in equal numbers and with distinct characters.

Occasional exceptions to both of the above rules have been found, however, and these have provided significant information as to the nature of the primary sex difference. Few animals produce exactly equal numbers of male and female offspring. In man, for example, slightly more males than females are born, (about 105 males to 100 females); in the fowl this ratio is reversed, and at hatching the females outnumber the males by about 100 to 94; while rarely the discrepancy in numbers may be even greater. These cases may represent occasional irregularities

in the mechanism which governs the production of the sexes or they may result from environmental influences or from differential mortality among the developing zygotes. The clear-cut distinction between the sexes is also subject to certain exceptions. Sometimes animals appear which are neither strictly male nor female but partake somewhat of the nature of both sexes. In extreme cases the same animal may contain both male and female reproductive organs and be thus a true *hermaphrodite*. Occasionally, in animals in which the sexes are usually quite distinct, an individual may be found which is sexually a composite structure or *gynandromorph* (Fig. 119, p. 317), a part of its body showing male characters and a part female. Recently many cases have been reported of animals which show intermediate or blended conditions of male and female characters. Series of such *intersexes* (Fig. 77, p. 218) have been found which show all the intergradations between maleness and femaleness and are completely sterile. Since maleness and femaleness may be present in the same animal, and especially since some animals may be neither male nor female, exhibiting instead a balanced or intermediate condition of the characters of both sexes, it is apparent that the sexual difference may be quantitative in its nature. In addition, therefore, to a simple mechanism controlling sex, the existence of which might be inferred from the usually discontinuous nature of the sex difference and from the production of the sexes in equal numbers, one may also expect to find other factors in which the sexes differ in degree. The inheritance and the determination of sex have, therefore, both *qualitative* and *quantitative* aspects, such as have been noted for other differentiating characters.

Secondary Sexual Characters.—In addition to the fundamental problem of sex *determination*, or the origin of the primary sexual difference, some explanation must also be sought for the *differentiation* of the sexes in traits which are intimately related to, and in many cases seem to be merely extended expressions of, the primary difference. The greater development of comb and wattles in male fowls and the more brilliant plumage of male birds in general (Fig. 68), the presence of horns in the males of some breeds of sheep and among deer, the mane of the male lion, facial hair and deep voice in men, and many other striking differences between males and females in structure and instincts are examples of what are commonly called *secondary sexual*

characters. These traits are inherited, but are limited in expression to a particular sex and are thus sometimes referred to as *sex-limited.* Their development appears to be dependent on the

FIG. 68.—Secondary sexual differences in conformation, comb form, plumage form and color in domestic fowls. Left, Silver Leghorn female; right, Silver Leghorn male. (*From Robinson.*)

sexual glands themselves, since if these glands are removed, by castration, such secondary characters may fail to appear, or if present may be greatly altered (Fig. 69). It is probable that the

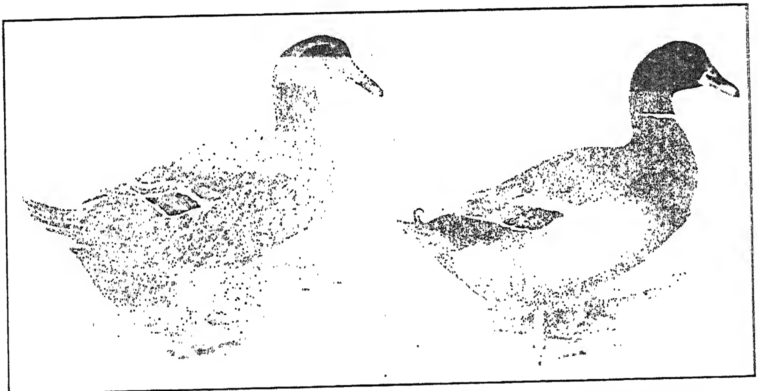


FIG. 69.—Effect of castration on secondary sexual characters in ducks. At left a normal Rouen duck; at right a Rouen duck from which the ovary was removed. The ovariotomized female has assumed male characters. (*From Goodale.*)

sexual glands, in addition to their reproductive functions, act also as glands of internal secretion and pour into the blood stream specific *hormones* which regulate the development of the second-

ary sexual characters. Although the study of such characters is throwing much light on the chemical nature of the sexual difference, the discussion here will be limited to the primary problem of sex determination.

The Causes of the Sex Difference.—The historical origin of the primary sex difference and the cause and meaning of its appearance have long caused speculations which at first found their expression in myth and legend, and which are still the subject of scientific debate. The nutrition of the mother or of the growing embryo, the age of the parents, the temperature or chemical constitution of the environment in which the embryo develops, the chemical composition of the egg, the period at which it is fertilized, and many other conditions have been suggested as playing a part in the determination of sex, but to review even the most important of these explanations would be of little value for our purpose, since many of them have been found to be either erroneous or secondary to the newer and simpler conception of sex determination. Here, the attempt will be made to present that theory of sex determination which at the present time is regarded by most biologists as the closest approach yet made to a satisfactory explanation. The fact that sex, at least in large part, has been clearly shown to be inherited like other mendelian traits has brought the problem definitely into the field of genetics, and has led to some very interesting discoveries as to the manner and mechanism of heredity.

The evidence upon which this theory of sex is based has been derived from two main sources—breeding experiments and a cytological study of the reproductive cells. Data obtained from each of these very diverse fields of investigation confirm that from the other and lead to the belief that a correct solution of the problem is approaching.

Evidence from Breeding Experiments.—The inheritance of sex itself evidently cannot be studied experimentally by the same methods used with other traits, for in most cases a cross between a male and a female produces offspring about half of which are males and half females. It is possible, however, to approach the problem of sex determination indirectly by studying the inheritance of a remarkable group of characters, which although not themselves concerned with the sexual process, have been found to be associated in a peculiar but quite definite fashion with the sex of the individual. These traits which,

except for their peculiar mode of inheritance resemble ordinary mendelian characters, appear to be linked with some of the factors which determine sex and are, therefore, known as *sex-linked* traits. Such traits have been studied in insects, birds, and mammals, including man, and they probably occur in most groups of animals. Their genetic behavior furnished one of the important clues which led to the development of the theory of sex determination which is generally accepted today.

A Case of Sex-linked Inheritance.—It will be well to describe in detail one of the first-discovered and best-known cases of sex-linked inheritance, that of red and white eye color in *Drosophila.* In the course of some breeding experiments with the normal wild type, which has red eyes, Morgan found one fly in which the eyes were white. This gave rise to a true breeding race of white-eyed flies. When he crossed this new variety with the wild, red-eyed type, Morgan discovered that the results obtained from a cross of a white male by a red female were quite different from those obtained from the reciprocal cross of red male by white female. This was the first case in which the results were found to depend on the sex of the parents in which the contrasted traits were introduced into the cross, for in ordinary mendelian inheritance, as has been seen, it makes no difference in either the F_1 or F_2 whether a given character is brought in by the male or the female parent. The details of these experiments, which have been repeated many times, are shown in Figs. 70 and 71. From the cross of white-eyed male with red female the first generation flies are red-eyed in both sexes (Fig. 70). When these are bred together, white reappears in a quarter of the F_2 offspring, indicating that red and white eye color are due to an allelomorphic pair of genes of which red acts as the dominant. However, of the F_2 offspring all of the females are red, while half of the males are red and half are white. The white male has transmitted his eye color only to his grandsons. These F_2 white-eyed males evidently carry no factors for red, since when bred with pure white stock, no red-eyed individuals ever appear among their offspring. The females, however, are apparently of two kinds, genotypically. When bred with pure red stock, half of them give nothing but red offspring and are thus pure for red, but the other half must carry some recessive white, for in their offspring *half* of the *males* are white eyed. These results are presented in the following table:

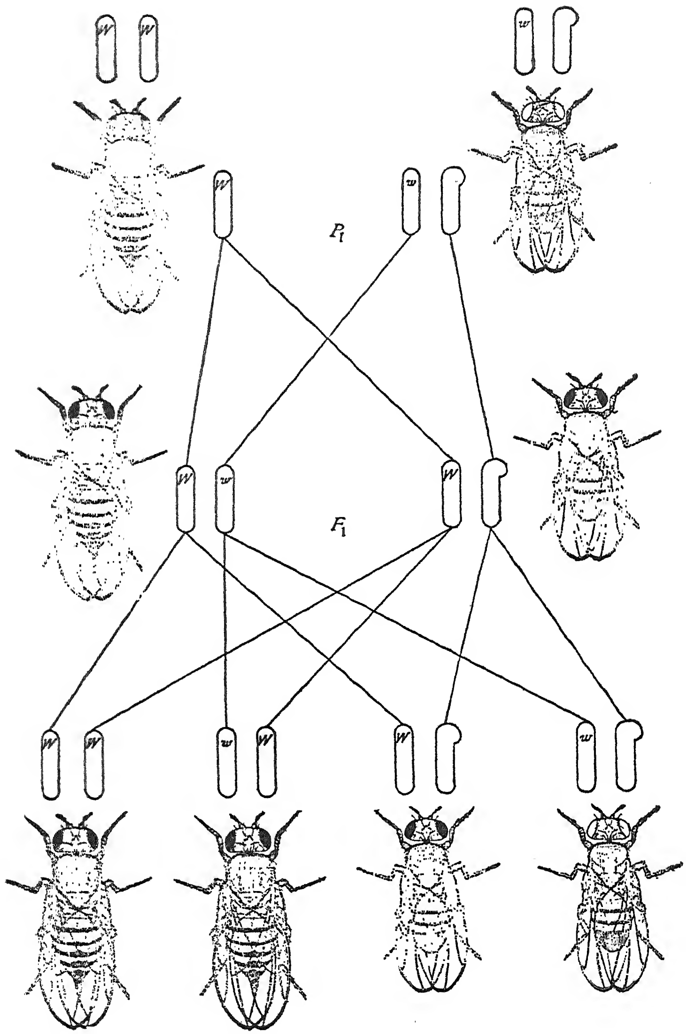


FIG. 70.—Sex-linked inheritance in *Drosophila*. The cross of red-eyed female by white-eyed male. The course of the sex-chromosomes carrying the sex-linked gene W-w is traced from parents to F_2. Females at left, males at right. (*From Morgan, Sturtevant, Muller and Bridges, courtesy Henry Holt and Co.*)

Parents.............	Red female × White male	
F_1..................	Females red	Males red
F_2..................	Females red	Males: One-half red, one-half white

When a red male is bred to a white female, however, quite a different result follows (Fig. 71). Among their F_1 offspring all the females are red-eyed and *all the males* are white-eyed. When these are bred together, their offspring (the F_2) consist of red-eyed and white-eyed individuals in about equal numbers in both sexes. All the white-eyed flies are apparently pure, for no red-eyed flies appear in their subsequent offspring; and the red-eyed *males* also breed true. The red-eyed F_1 females, however, must be heterozygous, for when bred to either white or red males, half of their male offspring are always white-eyed. These results are shown graphically in the following table:

Parents.............	White female	×	Red male
F_1..................	Females red		Males white
F_2..................	Females: One-half red, one-half white		Males: One-half red, one-half white

The inheritance of this character is so obviously related to sex as to suggest that a further analysis of the peculiarities of sex-linked inheritance may lead indirectly to conclusions on the inheritance of sex itself. A typical sex-linked trait in *Drosophila*, such as white eye color, is found to follow a peculiar type of *criss-cross* inheritance. A male transmits his sex-linked traits to his grandsons through his daughters. He never transmits them to or through his sons. The trait thus seems to alternate or cross from one sex to the other in its passage from generation to generation. Several dozen characters in *Drosophila* have been found to follow this method of inheritance, as well as many characters in certain other animals, including colorblindness, hemophilia, and other traits in man. All show the following peculiarities: (1) The female seems to exert a more pronounced effect both upon the F_1 and F_2 than does the male. If white eyes are introduced by the female parent, a half of both the F_1 and F_2 offspring are white-eyed; but if such a recessive trait is introduced by the male, it makes no appearance at all in F_1 and is found in only one quarter of the F_2. (2) Males are always pure for sex-linked traits and seem incapable of concealing recessive sex-linked factors. All red-eyed males, even those

from mothers which carry white, are pure red and cannot transmit white to their offspring; while red females may or may not

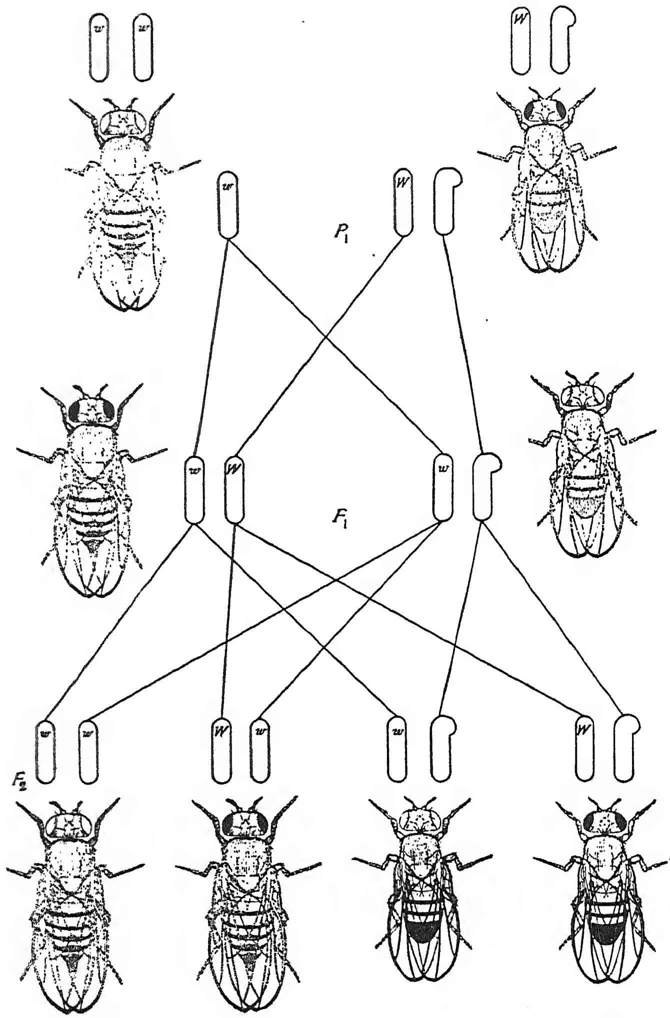


FIG. 71.—Sex-linked inheritance in *Drosophila*. The cross of white-eyed female by red-eyed male, the reciprocal of the cross shown in Fig. 70. Females at left, males at right. (*From Morgan, Sturtevant, Muller and Bridges, courtesy Henry Holt and Co.*)

carry white. (3) A recessive sex-linked trait appears more frequently in males than in females.

A study of these three facts suggests one important inference, namely, that the female may have *two* genes for any character linked with sex, and the male only *one*. On such an assumption the three features of sex-linked inheritance to which attention has been called may be explained: (1) A female with two genes for any trait may naturally be expected to have a greater influence than does a male in the transmission of this trait. (2) The possession of two genes evidently makes it possible for a female displaying a dominant trait to be heterozygous for it and thus to conceal a recessive gene, whereas the male, having but one, will necessarily breed true to the character which he shows. (3) The male, possessing but one gene, will display a recessive trait oftener than does a female, where the recessive gene may be present but masked by a dominant allelomorph.

Evidence from the Structure of the Gametes.—The breeding facts and the assumptions drawn from them thus suggest that the fundamental difference between the sexes may be due to a difference in the genetic constitution of the individual. What the nature of these entities is, the presence of two of which is associated with femaleness and of one with maleness, the breeding facts do not disclose. Fortunately, there is another and quite independent line of evidence which confirms and elaborates that supplied by studies of inheritance. This is derived from an investigation of the microscopic structure of the body cells and gametes of the two sexes.

About the time of the rediscovery of Mendel's laws it was shown that in certain insects there are two kinds of sperms, produced in equal numbers, one of which has an extra or *accessory* chromosome that is lacking in the other. The suggestion was soon made that this chromosomal difference in the male gametes is in some way related to the determination of sex, and that eggs fertilized by one type of sperm produced males and by the other type produced females.

The chromosomal constitution of the body cells and gametes in many species of animals at once became the subject of investigation. A considerable number of cases in insects and mammals were found in which there are two types of sperm, only one possessing the accessory chromosome; and this chromosome, often single and unpaired, and usually distinguishable from the others, was recognized in the body cells of male individuals. Still more significant was the discovery that in the body cells of female

individuals of these species there are *two* such accessory chromosomes, frequently recognizable by their size and shape as equivalents of the single one present in the male and distinguishable from the other chromosomes of the cell. They evidently constitute a pair, for in the reduction division they separate, and *every egg* contains one of them.

That there is a close relationship between these accessory chromosomes and sex was suggested by McClung in 1902 and is now generally admitted. They soon came to be known as the *sex chromosomes*, or X chromosomes, as distinguished from the others or *autosomes* which are present equally in both sexes. All eggs (in these species) are alike in containing such a chromo-

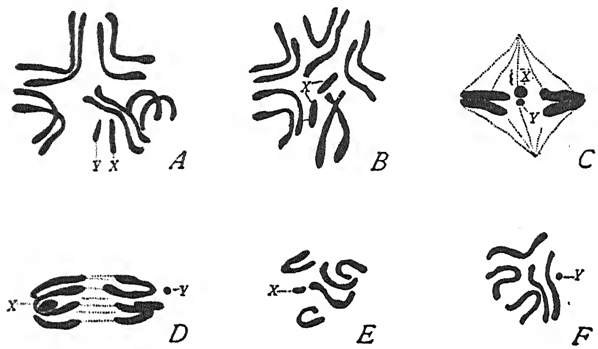


FIG. 72.—The chromosomes of a fly (*Calliphora*) showing X and Y chromosomes in (A) spermatogonia; (B) oogonia; (C) and (D) first spermatocyte (reduction) division; (E) and (F), X and Y spermatocytes after reduction.[1]

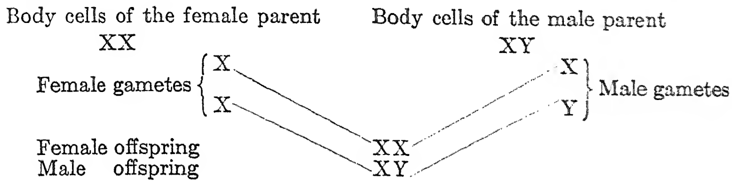
some, but there are two kinds of sperm, half of which carry it and half of which do not. The occurrence of two X chromosomes (as would result from the fertilization of an egg by a sperm which carried the X chromosome) seems to determine in some way the development of a female; the occurrence of only one (as would result from the fertilization of an egg by a sperm lacking this chromosome) seems to result in the development of a male.

These male-producing sperms sometimes simply lack the X chromosome and thus have a total chromosome number which is one less than that of the other sperms; or they may carry a mate to the X chromosome, quite different from it in appearance but which pairs with it before the reduction division and enters half of the male gametes (Fig. 72). This is the situa-

[1] From *The Cell in Development and Heredity*, by E. B. Wilson. Third edition, copyright 1925 by the Macmillan Company. Reprinted by permission.

tion, for example, in *Drosophila.* Such a body has been named the Y chromosome.

The female sex may, therefore, be represented by the formula XX and the male by X-, XO, or (as is more common) XY, these symbols standing for the sex chromosomes and their mates (if such occur). The behavior of these sex-determining elements in a cross, with the consequent production of equal numbers of male and female offspring, is shown in the following scheme:



Relation of Breeding Evidence to Cytological Evidence.—There is evidently a close parallelism between the behavior of these sex chromosomes, as determined by cytological study, and that of the sex-linked characters, as determined by breeding experiments. It has been seen that the peculiar inheritance of these sex-linked traits may be explained if it is assumed that, linked with them, there are two entities in the females and one in the males. The X chromosomes furnish precisely the mechanism which this assumption requires, and this has led to the hypothesis that *the genes for sex-linked traits are located in the sex chromosomes*, precisely as the genes for other traits are located in other chromosomes.

Sex Linkage of the XY Type.—Let us picture clearly the manner in which a sex-linked trait, such as white eye color in *Drosophila,* is transmitted in inheritance, bringing together the evidence both from breeding experiments and from cytological research.

The recessive gene for white eyes, it is assumed, is carried in the sex chromosome. If the sex chromosome is represented by X and the gene for white eyes by w, the genotype of a white-eyed male may be written (Xw) Y. Since the male contains only one X chromosome, its mate being the Y chromosome which in *Drosophila* carries no genes, such a fly can contain only one gene for white, and the two types of sperms which he produces may be written (Xw) and Y. The allelomorph of white is in this case the normal red eye, W, and the genotype of a red eyed female

may, therefore, be expressed by the formula $(XW)(XW)$. The results of crossing such a red-eyed female with a white-eyed male are shown in the following scheme:

Parents	Red female $(XW)(XW)$		White male (Xw) Y	
P_1 gametes	(XW)		(Xw)	Y
F_1	(XW) (Xw) Red female		(XW) Y Red male	
F_1 gametes	(XW)	(Xw)	(XW)	Y
F_2	(XW) (XW) Red female (homozygous)	(XW) (Xw) Red female (heterozygous)	(XW) Y Red male	(Xw) Y White male

The individuals produced by the union of an (XW) egg with an (Xw) sperm thus have two sex chromosomes and are therefore females; but since the X brought in by the sperm carried a gene for white eyes, these F_1 females are necessarily heterozygous for eye color, although appearing red-eyed because of the presence of a dominant red allelomorph of white. The F_1 males are all red-eyed, because the only X which they receive comes from their red-eyed mother.

In half of the eggs which these F_1 females produce, a white gene, w, is present in the sex chromosome, and in the other half its allelomorph, W; so that, as far as eye color is concerned, two types of eggs, (XW) and (Xw), are formed in equal numbers. Such a female, heterozygous for a sex-linked gene, is sometimes called a *carrier* for it, since she carries a recessive gene and may transmit it to her offspring, an ability which the male entirely lacks.

The F_1 males (like all males in this type of inheritance) produce two kinds of sperms, half of them carrying X (which in this case contains a W) and half carrying Y. If the two kinds of eggs and two kinds of sperms produced by the F_1 individuals unite at random, there will evidently be four possible types of offspring produced in equal numbers; (XW) with (XW), giving homozygous red females; (XW) with (Xw), giving heterozygous

red females; (XW) with Y, giving red males; and (Xw), with Y, giving white males. This is the result which, as has already been noted, actually does appear in the F_2 from this cross.

The cross of white-eyed female and red-eyed male is illustrated in the following diagram:

Parents	White female (Xw) (Xw)		Red male (XW) Y	
F_1 gametes	(Xw)		(XW)	Y
F_1	(XW) (Xw) Red female		(Xw) Y White male	
F_1 gametes	(XW)	(Xw)	(Xw)	Y
F_2	(XW) (Xw) Red female (heterozygous)	(Xw) (Xw) White female	(XW) Y Red male	(Xw) Y White male

Here the female F_1 individuals are heterozygous for red eyes, getting a white gene from their mother and the red allelomorph from their father. The male F_1 individuals, however, are all white-eyed, since the male derives its only sex chromosome, and hence all of its sex-linked traits, from its mother, which was white-eyed in this cross. In a cross between these two F_1 individuals there should evidently be four possible combinations of genes: (XW) with (Xw), giving a heterozygous red female; (Xw) with (Xw), giving a white female; (XW) with Y, giving a red male; and (Xw) with Y, giving a white male, and the results of breeding experiments fulfil this expectation.

The type of sex determination in which the male is heterozygous for sex-linked genes and contains X and Y chromosomes, while the female is homozygous and contains two X chromosomes, is known as the XY type of sex determination. This is the type found in many insects, in certain fish, and in most mammals which have been carefully studied. In man, Painter has found that the eggs all contain twenty-three autosomes and in addition one large X chromosome is present in each egg. The sperms, however, are of *two sorts;* half contain twenty-three autosomes and an X chromosome and half contain twenty-three autosomes and a Y chromosome. The scheme of sex determination in man is hence as follows:

	Female	Male	
	46 + 2X	46 + X + Y	
eggs	23 + X	23 + X	sperms
		23 + Y	
	46 + 2X female	46 + X + Y male	

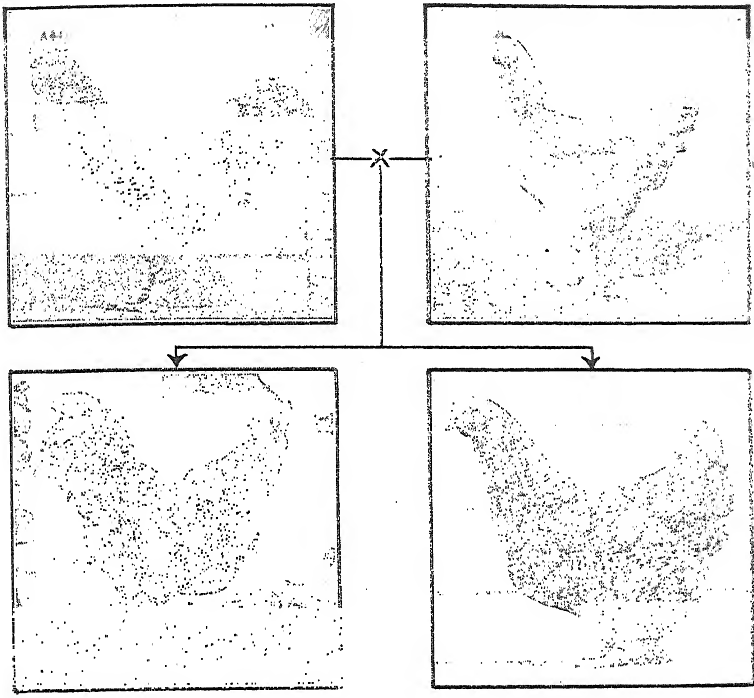
Sex in man is thus determined in the same way as in *Drosophila* and human sex-linked traits are inherited precisely like white eyes and other sex-linked traits in this animal.

Sex Linkage of the ZW Type.—In certain moths and birds, another type of sex determination has been found in which the male is homozygous for sex-linked traits and carries two sex chromosomes (commonly known as Z chromosomes) and the female is heterozygous for sex-linked traits, carrying one Z and (usually) one blank, or W, chromosome.

The inheritance of barred plumage in poultry is one of the best-known examples of this type. The barred pattern, as seen in such breeds as the Barred Plymouth Rock, is dominant over black or red unbarred plumage. Breeding evidence indicates that a male may carry two genes for barring but a female only one; and cytological research has shown that there are, indeed, two accessory or Z chromosomes in the cells of the male but only one in those of the female. If barred plumage is represented by B and non-barred plumage by b, the cross between a non-barred hen and a barred cock may be shown as follows:

P_1	Barred male (ZB) (ZB)		Non-barred female (Zb) W	
P_1 gametes	(ZB)		(Zb)	W
F_1	(ZB) (Zb) Barred male		(ZB) W Barred female	
F_1 gametes	(ZB)	(Zb)	(ZB)	W
F_2	(ZB) (ZB) Barred male (homozygous)	(ZB) (Zb) Barred male (heterozygous)	(ZB) W Barred female	(Zb) W Non-barred female

Here the F_1 birds of both sexes are barred, as are all of the F_2 cocks; but approximately half of the F_2 hens are barred and the other half are non-barred. This is the result obtained in actual breeding experiments (Fig. 73).



Barred male — Barred female

FIG. 73.—Sex linked inheritance in fowls. The cross of barred male by non-barred female.

The reciprocal cross of barred hen and non-barred cock gives, as might be expected, a very different result. The situation in this case is set forth in the accompanying diagram:

P_1		Non-barred male (*Zb*) (*Zb*)		Barred female (*ZB*) W
P_1 gametes		(*Zb*)	(*ZB*)	W
F_1		(*ZB*) (*Zb*) Barred male		(*Zb*) W Non-barred female
F_1 gametes	(*ZB*)	(*Zb*)	(*Zb*)	W
F_2	(*ZB*) (*Zb*) Barred male (heterozygous)	(*Zb*) (*Zb*) Non-barred male	(*ZB*) W Barred female	(*Zb*) W Non-barred female

Here the F_1 hens are all non-barred and the cocks all heterozygous barred; and in the F_2 there are equal numbers of barred and non-barred birds in both sexes. This, too, agrees with the breeding results (Fig. 74).

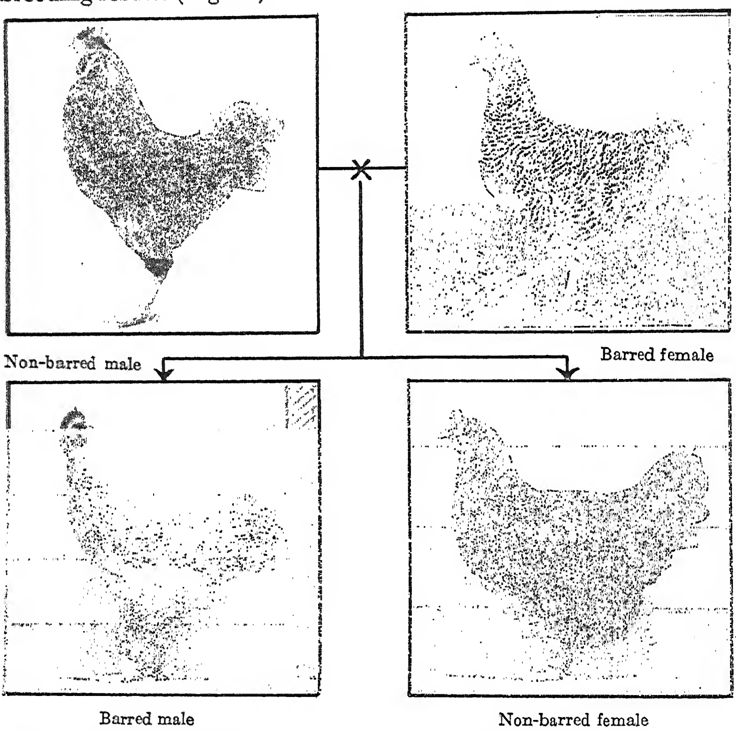


FIG. 74.—Sex linked inheritance in fowls. The cross of non-barred male by barred female, the reciprocal of the cross shown in Fig. 73.

In the fowl several other traits, such as rapid as contrasted with slow growth of the first plumage, and silver as contrasted with buff or golden plumage color, have been found to follow the same method of inheritance as barring, as also do several sex-linked characters in pigeons and canaries. In the currant moth *Abraxas*, cytological and genetic evidence both show that sex determination is of the ZW type. The distribution of this type among other animals and plants is not well known, since in only a few cases is there a combination of adequate cytological and breeding evidence.

The Chromosome Theory of Sex Determination.—There are, then, two kinds of evidence leading to the conclusion that the sex of an individual is determined by the chromosomal constitution of the gametes. There is, first, the cytological evidence that in many species of animals the chromosomes of the two sexes are not exactly alike. In *Drosophila*, in many other insects, and in mammals the female has in addition to a given number of autosomes, *two* sex or X chromosomes distinguishable by shape or behavior from the other chromosomes, while the male has but *one* X chromosome. In males the X chromosome has a mate, the Y chromosome, which is visibly different in shape and probably genetically different as well, from the X chromosome. In a few animals no Y chromosome has been found in the male, so that the females are XX, and the males are X. This chromosomal difference between the sexes results in the formation of different kinds of gametes. In the females, XX, the reduction division by which the gametes are formed results in the passage of one X to each egg, in the same way that one member of each pair of autosomes passes to each egg (page 141). In the males, XO or XY, only half the sperm can receive the X after the reduction division, while half of them either receive the Y chromosome or lack one chromosome entirely. The random union of X eggs with either X sperms or with Y (or O) sperms produces equal numbers of XX zygotes (females) and of XY (or XO) zygotes (males). In animals with the ZW type of sex determination the essential features are the same except that the female forms two kinds of eggs while all of the sperms are alike as to sex chromosomes. Thus sex is assumed to be *determined at fertilization* by the kind of chromosomes in the uniting gametes.

The second kind of evidence is from breeding experiments with sex-linked characters. The results show that the sexes are

different in respect to such characters, since the females (in *Drosophila*, some other insects, and mammals) may contain two genes for sex-linked traits while the males may contain but one such gene. The result is that all the eggs may contain such a gene while half the sperm contain it and half do not. The Y chromosome in these species probably carries no genes, although in some cases (fish and man) it is probable that the Y chromosome may carry some, which then show a peculiar type of inheritance from father to sons only. In the ZW type of sex determination the W chromosome corresponds to the Y and is not known to carry any genes. The assumption that sex-linked traits are located in the sex chromosomes explains their peculiar mode of inheritance and so fully confirms the conclusions from the cytological evidence that in breeding experiments sex-linked traits may be used as visible tags or markers by which the course of the sex chromosomes in inheritance may be followed with great accuracy.

Non-disjunction.—The conclusions with regard to the inheritance of both X chromosomes and sex-linked traits remained highly probable inferences from the close parallelism between the behavior of chromosomes and sex-linked genes, until in a specific case it was shown by Bridges that deviations from the usual rules of sex-linked inheritance in *Drosophila* were directly correlated with irregularities in the transmission of the X chromosomes. Ordinarily, as has been noted, white-eyed females bred to red-eyed males produce only red-eyed daughters and white-eyed sons. Bridges found that some females from a strain of white-eyed flies produced, when bred to red-eyed males, not only the expected classes of red daughters and white sons but also a few (about five per cent) of white daughters and red sons. He thought that these exceptions could be explained by assuming that in the oögenesis of the white-eyed females, both X chromosomes (each with a gene for white) occasionally stayed together at the reduction division, a process which he called *non-disjunction*, so that both went together into the polar body, resulting in an egg with no X chromosome; or, conversely, that both passed into one egg, which would then have two X chromosomes and thus two genes for white. The eggs of such a white female would then be not only the usual (Xw), but the exceptional kinds (Xw)(Xw) and (O). When fertilized by the Y sperm of the red male, the (Xw)(Xw) egg would produce a fly of genotype

$(Xw)(Xw)Y$ which having two X chromosomes would be a female and having two white genes would be white-eyed; conversely, when the no-X egg was fertilized by the (XW) sperm the resulting offspring would be $(XW)O$, and having but one X would be a red male. Thus the two exceptional classes of offspring could be accounted for. The white-eyed females produced by non-disjunction should then have two X chromosomes and one Y, and on microscopic examination Bridges found that this was so (Fig. 75). Breeding tests of such non-disjunctional females and cytological examination of their progeny have shown conclusively that the visible sex-linked trait has always the same distribution as the sex chromosome, which may be identified under the microscope. Non-disjunction, or the failure of two

Fig. 75.—The chromosomes of a male (XY), center; a normal female (XX), left; and a non-disjunctional female (XXY), right. (*From Sharp, after Morgan.*)

homologous chromosomes to separate at the reduction division, has since been noted in other chromosomes of *Drosophila*, and has probably occured in many other species, resulting in such chromosome aberrations as a doubling or tripling of the number of chromosomes which is characteristic of the gametes or somatic cells of the species. It is, therefore, not peculiar to the sex chromosome of *Drosophila*, although this case has provided the strongest evidence for identifying the sex-linked genes with the sex chromosomes.

Other evidence of this association is brought out by a study of the many sex-linked traits in *Drosophila*. Nearly fifty genes affecting eye color, wing form and venation, viability (Fig. 76), and other characters have been located in the sex chromosome. These show among themselves the same phenomena of crossing-over that ordinary non-sex-linked traits display. It has thus been possible to map the X chromosome in the same way as has been done for the others. Of further significance is the fact that breeding evidence shows crossing-over to take place, in *Droso-*

phila, only in the female and *never* in the male, a result which might have been anticipated from the circumstance that there are two homologous X chromosomes in the female but that the X

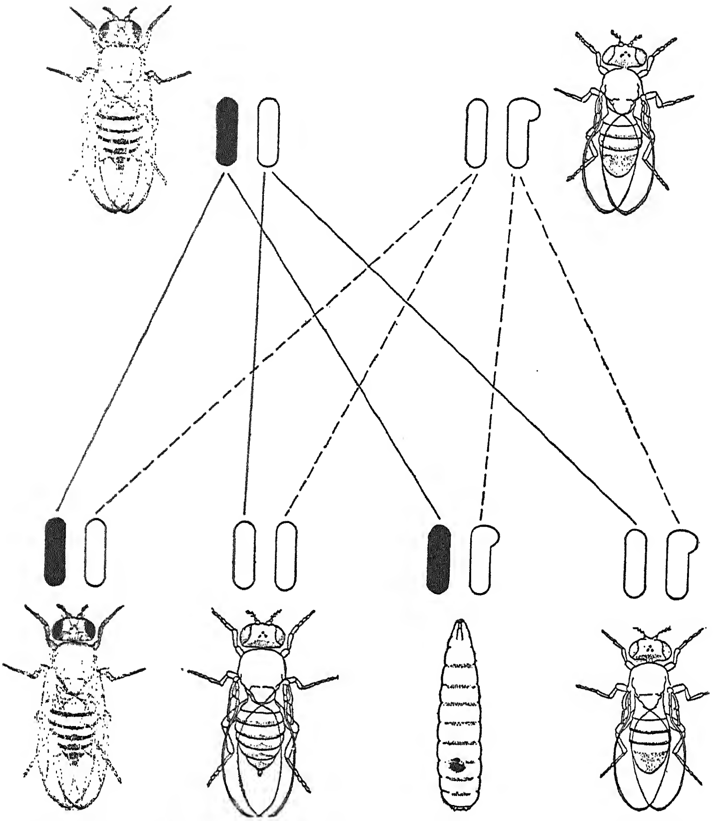


FIG. 76.—Diagram of the inheritance of a sex-linked lethal gene in *Drosophila* The sex chromosome carrying the lethal is black. The male offspring which receive this chromosome die in the larval stage from a tumor, so that among the flies actually hatched from such a mating there are twice as many females as males. The parents also carried the sex-linked genes for yellow body and eosin eye. (*From Morgan.*)

chromosome of the male has no similar mate, and that there seems to be no opportunity for interchange of material between the X and the Y chromosomes.[1] A similar situation exists in the fowl

[1] Not only is there no crossing-over of the sex-linked genes in the male of *Drosophila*, but none in any traits whatever. The condition is not readily explainable for the other chromosome pairs, however, and has been found in only one other animal.

and pigeon where crossing over between sex-linked characters occurs in the male, which has two sex chromosomes, but not in the female, which has but one.

This intensive study of sex-linked inheritance and of chromosome behavior in *Drosophila* reveals such a close parallelism between the two sets of phenomena (and these results have been confirmed by such evidence as is at hand from other animals) that the conclusion is necessarily reached that sex is definitely related to the presence of the sex chromosomes. These bodies, although resembling other chromosomes in being carriers of a long series of genes for diverse traits, are in addition able to influence the sex of the individual in which they occur. Maleness and femaleness, therefore, seem to differ from an ordinary pair of contrasted mendelian traits which are dependent for their expression on one or a few genes, and, instead, have their basis in the presence of one or of two entire chromosomes, each with its constitutent group of genes. Thus the male may be spoken of as heterozygous and the female as homozygous for sex, but it should be remembered that these terms here refer not to a single gene but to a much more complex physical basis.

Complications in the Problem of Sex Determination.—Some of the complexities involved are indicated by the careful studies of Goldschmidt and of Bridges on intersexes in a moth (*Lymantria*) and in *Drosophila*. Although the sex chromosomes of moths as indicated by the breeding evidence are of the ZW type of sex inheritance (female heterozygous) while *Drosophila* has the XY type (male heterozygous), experiments with the two different species have yielded similar results.

Intersexes in Moths.—In the gypsy moth (*Lymantria*) there is normally a sharp distinction between males and females in various characters, but by crossing the European and the Japanese species Goldschmidt was able to produce intersexes of practically all degrees between completely male and completely female types (Fig. 77). He has studied the various races of these two species and the types of intersexes from different crosses and has formulated an explanation for their occurrence. He recognizes the importance of the sex chromosomes, which he believes carry male-determining factors, but assumes the operation of another set of factors, female-determining in their activity, located either in the cytoplasm or in the W chromosome of the egg, which do not segregate but are transmitted only *from the*

female to her sons and daughters. Races differ in the "strength" of both the male and the female factors, and the sex of a given individual is determined by the balance between the activity of these two sets. This hypothesis is a factorial one, but the conditions which it assumes are much more complex than those involved in the activity of simple sex chromosomes, and it

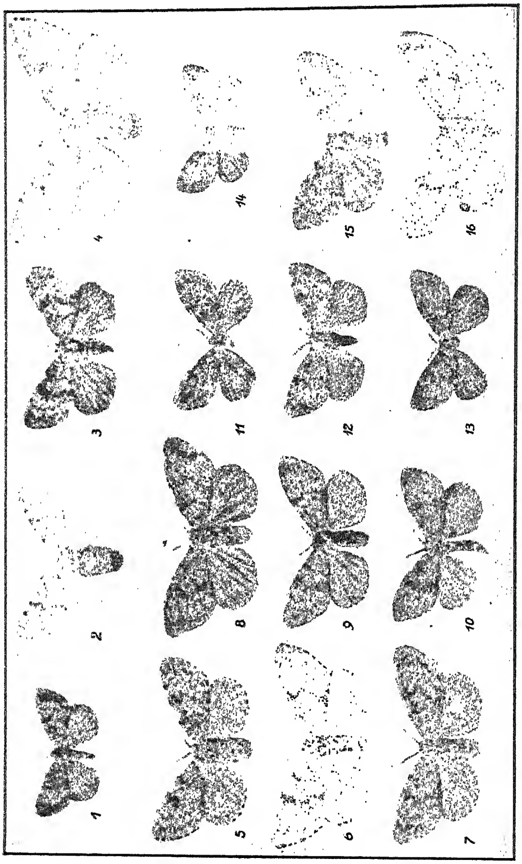


FIG. 77.—Intersexes of the gypsy moth (*Lymantria*). 1 and 2, male and female of European race (*L. dispar*); 3 and 4, male and female of Japanese race (*L. japonica*); 5–16, hybrids combining male and female characters. (*After Goldschmidt.*)

suggests the possibility of an influence of other agencies upon the expression of the various factors concerned.

Intersexes in Drosophila.—A similar indication that sex is the result of a balance between male-determining and female-determining agencies has been found by Bridges in *Drosophila*. He discovered a strain which continually produces intersexes

between males and females, readily recognizable and entirely sterile. Examination shows that these contain two X chromosomes and *three members of each set of autosomes.* Apparently, the X chromosomes are female-determining in their tendency but in some of the autosomes there are male determiners, and the *balance* between these decides the sex of an individual (Fig. 78). Where there are two X chromosomes and the autosomes are in sets of two, as normally, the animal is a female. If the X chromosomes are reduced from two to one, an ordinary male, as has been noted, is produced. If there are two X chromosomes

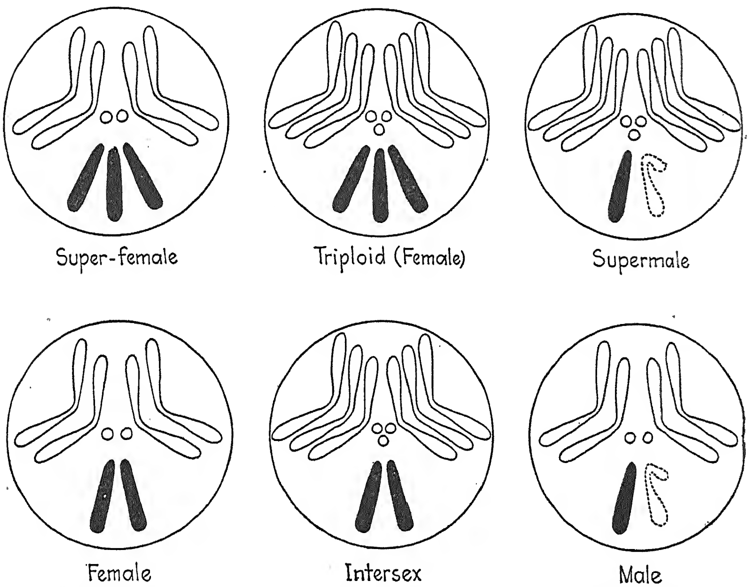


FIG. 78.—Effect on sex of the balance between X chromosomes (solid) and autosomes (outlined) in *Drosophila.*

but the autosomes are in sets of three, there is an excess of male tendencies but apparently not enough to produce a typical male, and an intersex is the result. Individuals with three X chromosomes and two autosomes in each set (superfemales) and with one X chromosome and three autosomes in each set (supermales) have been produced and recognized. It is evident that in *Drosophila,* at any rate, *all* the chromosomes, and not merely two of them, are concerned in the determination of sex.

A study of facts like these leads to the realization that sex determination is not quite so simple a matter as it was thought

to be when the sex chromosomes were first discovered. These bodies are undoubtedly important and in most cases seem to give the decisive stimulus in one direction or the other; but it must be recognized that sex is probably influenced by many factors in the other chromosomes or perhaps in the cytoplasm, and that there is probably a delicate balance between male-producing and female-producing tendencies which is ordinarily tipped one way or the other by the behavior of the sex chromosomes.

The determination of sex by forces other than those operating through the chromosomes has long been regarded as probable by many biologists. A number of cases have been brought forward in support of such a view, and some of these cannot be satisfactorily explained without some qualification of the chromosome theory in its simplest form.

The Freemartin.—It has long been known that when twins in cattle are of the same sex both animals are normal, but that when they happen to be of different sexes the male is normal but the other member of the pair, although outwardly more nearly like a female than a male, is usually sterile and in many respects is clearly intermediate between the two sexes. Such an individual is known as a "freemartin." By a study of a considerable number of such two-sexed twins in their embryonic condition, F. R. Lillie has proposed a hypothesis to explain these facts. He finds that, as the two embryos develop, they become crowded together in the uterus, with the result that their blood systems usually unite and blood from one embryo passes freely into the other (Fig. 79). The character of the embryos at an early stage indicates that one of them was destined (presumably by its genetic constitution) to be a male and the other to be a female. The sexual organs of the male, however, make their appearance before those of the female and secrete into the blood stream minute quantities of male hormones. It will be remembered from a previous discussion that many sex-limited traits are controlled by the presence of these sex hormones in the blood, introduced there from the sexual glands, a fact readily proved by the failure of such traits to develop after castration. What evidently happens in the freemartin is that hormones from the male twin enter the circulation of the female, check the differentiation of the female structures there, and tend to transform the animal into a male. The result of this conflict is the production of a sterile individual,

the freemartin, which is neither male nor female. The soundness of this conclusion is supported by the fact that occasionally there is no blood connection between twin embryos, and that when this occurs both members of a pair of two-sexed twins are normal in respect to sexual characters.

In cattle, therefore, the primary agency in the determination of sex probably lies in the chromosomes, but in the development of the individual this influence may be checked or even reversed by the activity (presumably chemical in its nature) of hormones or similar substances.

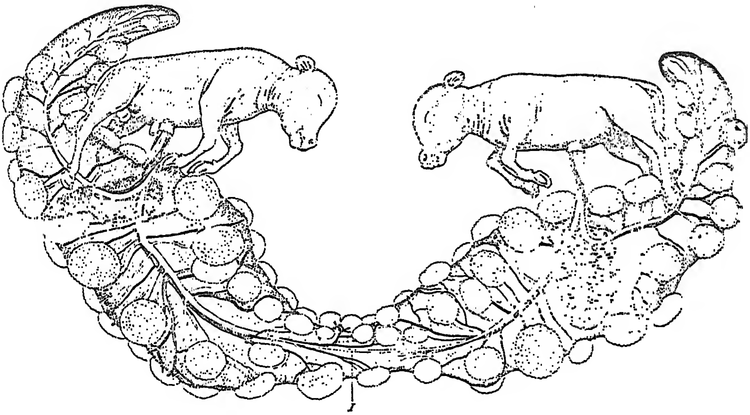


FIG. 79.—Opposite-sexed twin embryos in cattle. Normal male on the left and freemartin on the right. The artery connecting the two embryos is shown at (1). *(From Newman, after Lillie, courtesy of the University of Chicago Press.)*

Other Cases of Sex Reversal.—The idea that sex is not irrevocably determined at the moment of fertilization by the character of the gametes but that its expression may be influenced to a greater or less degree by various physiological conditions, is supported by evidence from other sources. Notable among these are instances of sex reversal which may occur not only in embryonic development but in adult life.

One of the most striking of these cases has recently been described by Crew. A purebred Buff Orpington hen, a good layer and the mother of chickens, ceased to lay, and shortly afterward it was noticed that she was beginning to crow. Her plumage was still like that of a typical hen, though her comb and wattles were unusually large. At this time she showed symptoms

usually associated with ovarian disease. She crowed weakly and her sexual behavior was indifferent. Shortly afterward she began to moult and her plumage, as it was renewed, was found to be that of a male. The following spring the bird was crowing lustily, resembled a normal male in appearance and behaved like a male toward cocks and hens. It mated with hens daily and was found to produce living spermatozoa. Finally, when bred to a virginal Buff Orpington hen, it became the father of two chicks.

Autopsy showed not only that the ovary had been almost completely destroyed by tubercular disease and replaced by a tumor, but the remarkable fact that two functional testes and their accompanying structures had made their appearance. In other words, this bird, which began life as a typical female, had become changed, structurally and functionally, into what was essentially a typical male. Riddle has recorded a somewhat similar case in pigeons.

This is perhaps the most extreme case of sex reversal yet recorded in poultry, but among the members of this group many other instances have been noted in which the removal or destruction of the female sexual organs by castration or disease has resulted in the loss of certain female traits and the acquisition of male ones. In explanation of these facts it has been assumed that the female is fundamentally a male but that the presence of female sexual organs and the secretion by them of hormones into the blood is able to inhibit the development of male traits and to produce those of the typical female, an exact reverse of the effect of the hormones from the male in the freemartin. Anything which removes the sexual glands results in a tendency for male characteristics to make their appearance again.

Metabolic Theories of Sex.—If sex may be modified or reversed by the presence of minute quantities of chemical substances such as the sex hormones, why is it not possible that all sex differences may depend on chemical alterations rather than on the chromosomal structure of the gametes?

The metabolic theory of sex, as developed by Riddle and others, indeed regards sex in animals as the result of plastic or reversible *physiological* processes rather than as being completely determined by fixed *morphological* differences in the gametes.

Before discussing this theory, the distinction between *sex determination* and *sex differentiation* which was outlined earlier in

the chapter must again be emphasized. When it is said that sex is *determined* at fertilization, it is meant that the mechanism of inheritance, the chromosomes, provides for the distribution to the gametes of certain hereditary potentialities which react to a given set of conditions in a specific way just as do other genetic factors. The specific reaction in the one case is the development of testes which produce sperm and in the other case the development of ovaries which produce eggs. The *differentiation* of sex refers to the future development of these potentialities and the divergence of the sexes in other sexual characters.

There is a good deal of evidence that males and females differ in many ways in addition to the chromosome differences which they show. The chief difference is that the female is often characterized by a comparatively low rate of metabolism; the male by a higher one. Riddle has found a similar difference between the male-producing and female-producing gametes of pigeons. Here two eggs are laid at a time, and in some species one more commonly develops into a male and the other into a female. He finds that the female-producing egg is characteristically larger, has a lower water content, a greater amount of stored food, and a lower rate of metabolic activity than the male-producing egg (Fig. 80). The female pigeon is known from genetic evidence to be heterozygous for sex and to produce approximately equal numbers of male-producing and female-producing eggs, so that the physiological differences are in agreement with the genetic facts. However, if the eggs are continually removed and the female, instead of being allowed to incubate her eggs, is forced to lay more frequently, *both* eggs of the pair show the chemical constitution of female-producing eggs and both develop into females. Riddle believes that such reproductive overwork on the part of the mother is accompanied by changes in the metabolism of her gametes in such a way that the egg which normally would produce a male and which apparently has the chromosomal constitution of a male now develops into a female.

A somewhat similar result has been obtained with poultry by Jull, who found that the proportion of males was much higher from the early eggs laid by a pullet, but decreased steadily among the offspring from later eggs laid after a longer period of egg production. The relation between the proportion of males and the antecedent egg production of the mother is given in Table IX.

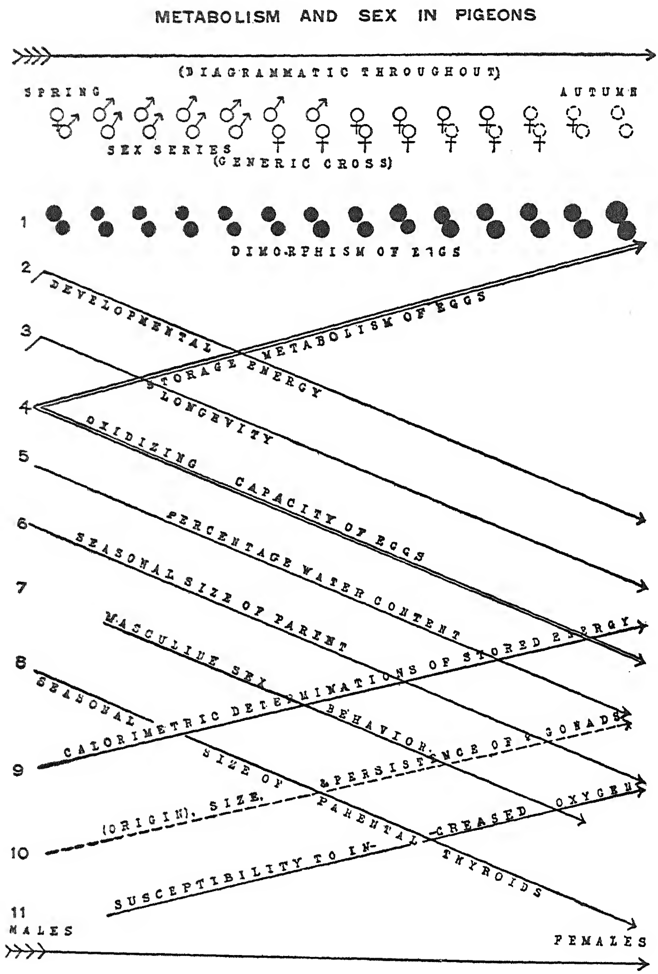


FIG. 80.—Chart of the Metabolic Theory of sex as applied to pigeons. Progression from the left to the right side of the chart represents advance of the season from spring to autumn, and increasing femaleness of the embryos produced. The lines (2, 3, 4 etc.,) represent the general tendencies of various qualities and processes assumed to be related to sex. The lines which slope upward indicate increase; those which slope downward indicate decrease. (*From Riddle.*)

TABLE IX.—THE RELATION BETWEEN ANTECEDENT EGG PRODUCTION AND SEX RATIO IN THE FOWL. FAMILIES OF 10 OR MORE OFFSPRING
(*Data from Jull*)

Antecedent egg production of mother		Sex of resulting chickens		
Class range	Average eggs	Females	Males	Percentage of males
0– 20	4.79	102	173	62.91
21– 40	27.86	94	127	57.46
41– 60	47.85	165	135	45.00
61– 80	69.45	108	87	44.61
81–100	88.92	101	61	37.65
101–120	114.50	80	38	32.20

These observations have been interpreted as showing that the difference between the sexes is to be regarded as quantitative, a conclusion which seems to be similar to Goldschmidt's and Bridges' later theory of sex as a balance between genetic tendencies toward maleness and femaleness. Riddle believes that sex is due to differences in metabolic level, and is thus reversible and dependent on the metabolic condition of the mother. Jull presents an alternative suggestion in explanation of his data, namely, that among the early eggs laid by a pullet, the W chromosome, which is found in female-producing eggs, is extruded into the polar body more frequently than the male-determining sex chromosome (Z) instead of with the equal frequency determined by chance assortment, as is ordinarily the case; and that the reverse situation occurs later. He suggests that such differences in oögenesis may be caused by chemical changes in the gametes produced after considerable antecedent egg production.

Both interpretations assume that chemical changes may affect the processes involved in sex determination and differentiation; and both assume a normal sexual dimorphism among the eggs of birds in harmony with the facts from cytology and genetics.

The metabolic theory supposes that the chromosomal mechanism of sex determination normally starts the individual in a male or a female direction by the early establishment of a male or a female metabolic level, and that in some cases the chromosomal mechanism may be overridden and the sexual characters altered

by physiological factors, as in the freemartin. The chromosome theory maintains that since the direction of development is determined by the chromosomes, this is the primary method of sex determination and that the metabolic differences are secondary. Thus the two theories are complementary, rather than diametrically opposed, since one accounts for the morphological, the other for the physiological, basis of sex.

Conclusion on Sex Determination.—It would be surprising indeed if a character like sex were not affected by many factors in the organism and in the environment, for it has been found to be the rule that no character is completely determined by a single factor, but that its appearance is an expression of a balance between a complex set of internal and environmental conditions. Sex is apparently no exception to this rule. The fundamental differences between the sexes are probably chromosomal, and the chief factors affecting sex are located in the sex chromosomes. Sex is also influenced, however, by other agencies. According to the theories of Bridges and of Goldschmidt, sex is primarily the result of a balance between two such sets of factors, aided possibly by other forces. An individual "determined" or started in the male or female direction may undergo very different development, and the original sex tendency may even be reversed if the balance is disturbed by chromosome irregularities, if the chemical products of the sex glands themselves are either eliminated or altered, or if various environmental factors act to change the expression of the sex determining factors. The whole subject of sex determination and differentiation is being actively investigated at present, and it will not be possible to speak with authority on this subject until more evidence from breeding experiments and cytological observations is at hand.

QUESTIONS FOR THOUGHT AND DISCUSSION

88. In man, there are about 105 males born to every 100 females. To what cause or causes may this be due?

89. In several animals, if the length of the sperms is measured and plotted, a bimodal curve results. What is the probable explanation of this fact?

90. From what you have learned of the chromosome mechanism of crossing-over and sex determination, suggest at least one reason why there is no crossing-over of any genes in the male of *Drosophila*.

91. If a factor for high egg production and one for barring are both sex-linked traits, of what practical importance would this be to the poultry breeder?

92. It is ordinarily impossible to determine the sex of young chicks, although it would be very useful to be able to do so. The difference between barred and non-barred birds, however, can be told at the time of hatching. How could this fact be utilized in certain cases to distinguish the sex of the newly hatched chicks?

93. What effect on the sex ratio would a recessive sex-linked lethal factor have in man?

94. Do you think that the nutrition of the mother has any effect on the sex of her offspring? Explain.

95. What prospect is there for influencing the sex of unborn offspring in man?

96. It has been found in pigeons that eggs with a relatively large amount of stored food and a relatively low metabolic rate tend to produce females, and that those with less storage and higher metabolic rate, produce males. With what general characteristics of maleness and femaleness may these differences in germ cells be related?

97. What evidence do you know of in man that sex is quantitative and that there are various degrees of maleness and femaleness?

98. Sex chromosomes have been found in very few species of plants. Suggest an explanation for this.

PROBLEMS

Note.—In all problems involving sex-linked characters state results for the two sexes separately.

187. In *Drosophila,* if a white-eyed female is crossed with a red-eyed male, and if a F_1 female from this cross is mated with her father and an F_1 male with his mother, what will be the appearance of the offspring of these last two crosses as to eye color?

188. In *Drosophila,* if a homozygous red-eyed female is crossed with a white-eyed male, and if an F_1 female from this cross is mated with her father and an F_1 male with his mother, what will be the appearance of the offspring of these last two crosses as to eye color?

189. In *Drosophila,* if a white-eyed female is crossed with a red-eyed male and the F_2 from this cross allowed to interbreed freely, what will be the appearance of the F_3 as to eye color?

190. In *Drosophila,* if a homozygous red-eyed female is crossed with a white-eyed male and the F_2 allowed to interbreed freely, what will be the appearance of the F_3 as to eye color?

191. In *Drosophila*, vestigial wings (v) are recessive to the normal long wings (V) and the gene for this trait is not in the sex chromosome. If a homozygous white, long female is crossed with a homozygous red, vestigial male, what will be the appearance of the F_1? of the F_2? of the offspring of a cross of the F_1 back on each parent?

192. In *Drosophila*, what will be the appearance of the offspring of the following crosses:

$$(XW)(Xw)Vv \times (Xw)Y\ vv.$$
$$(Xw)(Xw)Vv \times (XW)Y\ Vv.$$

193. In *Drosophila*, two red-eyed, long-winged flies when bred together produce the following offspring:

Females: three-fourths red, long; one-fourth red, vestigial.

Males: three-eighths red, long; three-eighths white, long; one-eighth red, vestigial; one-eighth white, vestigial.

What are the genotypes of the parents?

194. In *Drosophila*, a cross between a red, vestigial female and a white, long male produces offspring in which, both among males and females, there are approximately equal numbers of red, long; red, vestigial; white, long; and white, vestigial flies. If two of these red, long flies are bred together, what will be the appearance of their offspring?

195. In *Drosophila*, white eye color and club wing are both sex-linked with a cross-over value of about 15 per cent. If a wild-type female (red, long) is crossed with a white, club male, what will be the appearance of the offspring? If both males and females of the F_1 are crossed back to pure white, club stock, what will be the offspring in each case?

196. In *Drosophila*, yellow body is sex-linked and recessive to the gray body of the wild fly. Vermillion eye is also sex-linked and recessive to the wild red eye. The genes for yellow and vermillion show about 28 per cent of crossing over. The gene for vestigial wings is in one of the autosomes. If a homozygous yellow-bodied, red-eyed, long-winged female is crossed with a homozygous gray-bodied, vermilion-eyed, vestigial-winged male; and if an F_1 female is crossed with a yellow, vermilion, vestigial male, what will be the appearance of the offspring of this last cross?

197. A girl of normal vision whose father was color-blind marries a man of normal vision whose father was also color-blind. What type of vision will be expected in their offspring?

198. A color-blind man marries a woman of normal vision. They have sons and daughters, all of normal vision and all of whom marry normal persons. Where among the grandchildren may color blindness be expected to appear? If there are cousin marriages among these grandchildren, where among *their* offspring may color blindness be expected to appear?

199. A man and woman, both of normal vision have (1) a color-blind son who has a daughter of normal vision; (2) a daughter of normal vision who has one color-blind and one normal son; and (3) another daughter of normal vision who has five sons, all normal. What are the probable genotypes of grandparents, children, and grandchildren?

Note.—In the following problems assume that right-handedness (R) is dominant over left-handedness (r), and brown eye color (B) over blue (b).

200. A brown-eyed woman with normal vision whose father was color-blind and blue-eyed marries a man who is blue-eyed and of normal vision. What offspring may this couple expect, as to eye color and vision?

Note.—Let c stand for the gene for color-blindness and C for its normal allelomorph.

201. If a woman with the genotype $Rr\ Bb$ (XC) (Xc) marries a man who is $Rr\ bb$ (Xc) Y, what chance will their daughters have of being right-handed, blue-eyed, and color-blind?

202. In poultry, if a non-barred cock is crossed with a barred hen, and an F_1 female from this cross is mated with her father and an F_1 male with his mother, what will be the appearance of the offspring of these last two crosses, as to barring?

203. In poultry, if a homozygous barred cock is crossed with a non-barred hen and if an F_1 female from this cross is mated with her father and an F_1 male with his mother, what will be the appearance of the offspring of these last two crosses, as to barring?

204. In poultry, if a non-barred cock is crossed with a barred hen, and an F_2 from this cross is allowed to interbreed freely, what will be the appearance of the F_3 as to barring?

205. If a homozygous rose-comb, barred cock is crossed with a homozygous pea-comb, non-barred hen, what will be the appearance of the F_1? of the F_2? of the F_1 crossed back with each parent?

206. If a homozygous barred, rose-comb cock is crossed with a non-barred, single-comb hen, what will be the appearance of the F_1? of the F_2? of the F_1 crossed back with each parent?

207. A single-comb barred cock crossed with a walnut-comb, barred hen produces the following offspring:

4 rose, barred males.
5 walnut, barred males.
2 rose, barred females.
3 rose, non-barred females.
2 walnut, barred females.
2 walnut, non-barred females.

What are the genotypes of the parents?

208. A rose-comb, barred cock mated to a single-comb, barred hen produces the following offspring:

12 rose, barred males.
11 single, barred males.
5 rose, barred females.
6 rose, non-barred females.
7 single, barred females.
4 single, non-barred females.

If both these parent birds were crossed with pure single-comb, non-barred stock, what would their offspring be, as to comb and barring?

209. In fowls, late feathering (L) is sex-linked and dominant to early feathering (l). Give the appearance and genotype of the progeny of matings between the following homozygous individuals:

(1) Late, barred male × early, non-barred female.
(2) Early, barred male × late, non-barred female.
(3) Early, non-barred male × late barred female.

210. Assume that L and B show 20 per cent of crossing-over (in the male only). If one of the male offspring from cross (1) of the preceding question is mated with an early, non-barred female, what will be the appearance of their offspring as to feathering and barring?

211. If a white-eyed, non-disjunctional female *Drosophila*, (Xw)(Xw)Y, is mated to a red-eyed male, what kinds of offspring may be expected as to sex and eye color?

212. If a hen which undergoes sex reversal, and thus becomes a functional male, produces gametes of the same chromosomal constitution as before (although they are now sperms instead of eggs), what will be the sex of her offspring when she is mated with a normal hen?

213. If such a sex-reversed hen were barred, what would be the appearance of her offspring when bred to a non-barred hen?

214. In a small fish (*Aplocheilus*) the wild form is brown; other varieties are blue, red, and white. Sex determination is of the XY type (male heterozygous) as in *Drosophila*. The following results of crossing these varieties were obtained by Aida:[1]

Cross 1

P_1 White ♀ × Red ♂

F_1 All red

F_2	Red ♀	White ♀	Red ♂	White ♂
	41	43	76	0

[1] In the second cross three exceptional individuals have been omitted.

Cross 2

White ♀ × F_1 Red ♂ (from Cross 1)

Red ♀	White ♀	Red ♂	White ♂
0	197	251	0

Cross 3

P_1 Red ♀ × White ♂

F_1 All red

	Red ♀	White ♀	Red ♂	White ♂
F_2	87	0	42	33

What is the method of inheritance of red and white color? Draw up a factorial chart to make your explanation clear, and compare the actual numbers in each class with the numbers to be expected on your hypothesis.

215. In *Aplocheilus*, these further results were obtained by Aida. Sex in these fishes cannot be distinguished until they are a year old, so that sex distribution can only be given for those which live to this age:

P_1 White ♀ × Brown ♂

F_1 All brown

F_2....................	Brown		Blue		Red		White	
Total young............	248		57		53		21	
Sex of survivors.........	♀	♂	♀	♂	♀	♂	♀	♂
	77	147	56	0	9	37	19	0

Explain the inheritance and the genetic relations of brown, blue, red, and white. Make a factorial chart as in the previous problem, comparing the actual numbers in each class with the numbers expected on your hypothesis.

216. A factor l in *Drosophila* is recessive, lethal, and sex-linked. If female Ll is crossed with a normal male, what should be the sex ratio of the progeny?

217. In fowls a factor K is recessive and sex-linked. All zygotes pure for K die before hatching. A male heterozygous for this factor is crossed with normal females and produces 120 live chickens. How many of these would you expect to be males and how many females?

218. In Goldschmidt's hypothesis of sex determination in the gypsy moth, he assumes that sex is due to a balance between a factor for maleness, M, which occurs in the sex chromosomes, and a factor for femaleness, F, which is presumably located in the cytoplasm of the egg and can therefore be transmitted only *through the female.* Gypsy moths have the ZW type of sex determination, so that the male possesses two male factors (MM) and the female only one (M). Goldschmidt assumes that in different races of gypsy moths there are different values

or strengths displayed by the M and F factors. If in a given individual the value of F is greater than that of the sum of the M factors, the individual becomes a female; if the sum of M is greater than F, it becomes a male; and if the two are equal, it is an intersex. To a certain "weak" race Goldschmidt assigns the value 80 to F and 60 to M, so that the females are $F(80)$ $M(60)$ and the males are $F(80)$ $M(60)$ $M(60)$; and to a certain "strong" race the value 100 to F and 80 to M, so that the females are $F(100)$ $M(80)$ and the males $F(100)$ $M(80)$ $M(80)$.

What will be the sex of the offspring if a "strong" female is crossed with a "weak" male? If a "weak" female is crossed with a "strong" male?

219. If a triploid female fruit fly (Fig. 78) is crossed with a normal male, what will be the chromosomal constitution of each of the twelve types of offspring produced. Identify among these the six types shown in Fig. 78, and state the probable sexual character of the others. (In the reduction division, the members of a set of three chromosomes are separated, two going to one pole and one to the other. Reduction in each set of chromosomes is independent of that in the others.)

REFERENCE ASSIGNMENTS

62. What evolutionary advantages and what disadvantages has sexual reproduction as compared with asexual multiplication?

63. Describe Darwin's theory of sexual selection.

64. Compare the effects of castration in mammals and birds.

65. Compile a list of ten animal species showing the XY type of sex determination; five species showing the XO type; and three species showing the ZW type.

66. State Morgan's "elimination" theory for the origin of gynandromorphs in *Drosophila*.

67. In honeybees the fertile female or queen mates only once. Her later offspring are mostly females. Explain.

68. Describe a case where sex reversal normally occurs in the life history of an animal.

69. What evidence is there as to sex determination in dioecious plants?

70. Give an account of the occurrence of sex-linkage in a plant gametophyte, as reported by Allen.

71. Give the derivation of the following terms and explain in what way each is appropriate:

Autosome	Gynandromorph
Hermaphrodite	Parthenogenesis

CHAPTER X

THE INHERITANCE OF QUANTITATIVE CHARACTERS

All of the characteristics of plants, animals, and man which have thus far been considered are definite and distinguishable traits. Such characters as Mendel investigated in peas, the four types of comb in poultry, the various coat colors of mice, most of the mutant forms of *Drosophila* and many other traits which show alternative inheritance are readily distinguished by contrast with their opposites. Factor interaction, linkage, and other causes may introduce complications in their inheritance, but the classification of a given segregating population and a determination of the ratios which it exhibits are for the most part easy matters, however difficult a correct interpretation of these facts may prove to be. In a cross between a wild, gray, house mouse, for example, and a pale, pink-eyed, spotted, brown one, segregation and recombination will produce a wide range of different coat colors in F_2, but each is a distinct type and with but little practice may be placed in its proper class. Such traits involve differences in some *quality* of the individual, such as color, form, or texture, and hence are commonly referred to as *qualitative* characters. It is with these that students of mendelian inheritance have been chiefly concerned.

Quantitative Characters.—Even a casual observation of living things, however, will disclose a great many traits which are not differences in quality but in *quantity*. Two individuals or two races may resemble each other in color and in form, but may differ greatly in size. Examples of such *quantitative* characters are those involving the length, weight, and girths of the body; the number of multiple parts, such as petals or appendages; degree of fertility, yield, intelligence, strength, or development in any other character, including most of those which are of importance from an economic point of view. It is obvious that characters of this sort involve differences in *degree* rather than in *kind*, and are, therefore, not definite and clearly distinguishable, as are qualitative ones. In studying body

height, for example, it is impossible to divide men into "tall" and "short," or even into "tall," "medium," and "short," for if a large random group of people are examined, it will not be found to be composed of definite groups, but of individuals representing every gradation in height from very short to very tall.

In the inheritance of such characters, also, the same absence of clearly marked classes is found. If a homozygous "large" individual is crossed with a homozygous "small" one, the F_1 is ordinarily intermediate and fairly uniform, but the F_2, if extensive enough, includes some individuals as small as one grandparent, some as large as the other, and others ranging all the way between (Fig. 81). Here there is evidently no clean-cut

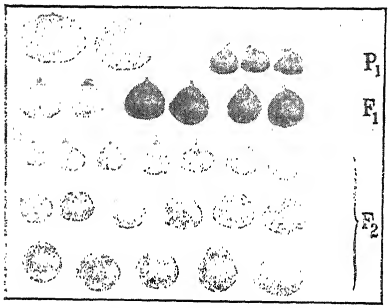


FIG. 81.—Inheritance of size in chestnuts. The two parent types are shown above: nuts from the F_1 trees below; followed by representative nuts from the F_2 trees. *(From Detlefsen, in Journal of Heredity.)*

segregation into distinct classes which can be recognized and counted, and the problem of determining the method of inheritance of such characters must evidently be approached by a somewhat different method from that of ordinary mendelian analysis. Indeed, such characters were long thought to constitute important exceptions to Mendel's laws and to require some other principle for their explanation.

In recent years, however, it has been recognized that even these quantitative characters are not essentially different in their method of inheritance from the more definite ones on which Mendel based his theory. The extension of mendelian principles to this very important group of traits is one of the notable advances which genetics has made since Mendel's day, and a brief discussion of the modern conception of the inheritance of quantitative characters will be presented in this chapter.

Methods of Analysis of Quantitative Characters (Biometry).—It is clear that these traits cannot readily be described by words, such as "tall," "short," "heavy," "light," "high," "low," "weak," "strong," or others, because of the existence of all grades of intermediate conditions. Evidently, the only way in which a satisfactory determination and description of such characters can be made is by *measurements*. Characters involving height may be stated in centimeters; of weight, in kilograms; of yield, in liters, and so on. By this means every individual has a definite quantitative description of its particular character whereby it may easily be compared with other individuals of the same kind. The series of measurements which have thus been gathered in any study of the inheritance of size must then be classified and simplified by methods of statistical analysis if they are to be handled easily and their meaning presented in precise and understandable form. The application of statistical methods to living things is known as *biometry* and has developed into an important branch of biological investigation. Before it is possible to understand the inheritance of quantitative characters it is necessary therefore, to master certain of the more important methods of biometrical analysis and learn to extract from the "raw" data themselves a few of the simplified measures, or *constants*, which are commonly used in problems of this sort. The concern here is with biometry not as an end in itself, but as a convenient mathematical tool which may be used in dealing with quantitative characters.

Biometrical Constants.—Even in a group of individuals which is known to be homozygous for a given size character, all the members are not exactly alike, for quantitative characters, perhaps even more than qualitative ones, are influenced in their expression by the environment. Bean plants belonging to the same pure line or race, for example, which are similar in their entire genetic constitution, differ markedly in vine height, pod size, yield of fruit, and other quantitative traits according to whether or not they have been grown under those conditions of temperature, moisture, and soil fertility which stimulate a vigorous development of the various bodily structures. Similarly among animals, proper feeding results, even in the same race, in a much greater development of such characters as body weight, milk production, and egg yield than does a ration which is deficient in some component necessary to maximum development. Even when

every attempt is made to secure complete uniformity, both in the genetic constitution of the individuals studied and in the various factors of their environment, there is almost always some slight variation among them with regard to any quantitative character. If the inheritance of such a character is to be studied by crossing individuals from one group with those from another (tall plants with dwarf ones, say) and the results of this cross followed to later generations, it is important to obtain a single quantity which shall represent, as accurately as possible, that size character for that particular group, free from the fluctuations shown by individual members. Such a quantity is the *average* or *mean*, and its determination for a given group is an important step in biometrical analysis.

It is also useful to obtain a measurement of the *variation* which a given group of individuals displays, for not only does this often serve to indicate purity of type, or influence of the environment, but a study of the comparative variability of parents and offspring has given valuable clues as to the method of inheritance of quantitative characters. The mean tells nothing of variation, for two populations may have the same mean but may differ greatly in the extent to which their members vary around it; and other constants, especially the *standard deviation* and the *coefficient of variability*, must be determined.

Measurements of type and measurement of variation are thus two of the primary objects of a biometrical analysis of size inheritance or, indeed, of any statistical study of quantitative characters. The method by which these two quantities are determined will now be briefly described.

Measurement.—The first step, obviously, is to measure carefully all the individuals of the particular group which is to be studied. That these original measurements should be made as accurately as possible goes without saying. No amount of statistical treatment will ever evolve sound results from unsound data. It should always be borne in mind that the biometrical analysis of a mass of data adds nothing new thereto but merely reduces these data to a simpler form wherein we may be able to perceive certain fundamental relationships which might otherwise escape observation.

Classification.—The first step in simplifying the large and often confusing array of figures which results from the measurement of a group of individuals with regard to a given size character is to

arrange and classify them in a systematic fashion. In the figures for weight of 200 men, for example, which are given in Table XVII, at the end of this chapter, the lightest individual weighs 95 pounds and the others are scattered all the way along between that figure and the weight of the heaviest man, 195 pounds. If these 200 measurements are arranged in order, something has been done to simplify matters, but a much clearer picture of the make-up of this particular group of men as far as weight is concerned is obtained, if, instead of studying these men as individuals, each of them differing from every other, they are divided into a comparatively small number of *groups* or *classes*, placing together in each class those who are nearly alike in body weight. In such a *frequency distribution* the relative number of individuals who are light, who are heavy, or who hold any given intermediate position are seen at a glance. What the limits of the classes are, provided the classes are of equal value, makes no great difference, although, of course, the division of a population into a large number of classes with narrow limits gives a correspondingly more accurate picture of its composition than a division into a smaller number of relatively wide classes.

In Table X, the 200 weights presented in Table XVII have been arranged into eleven 10-pound classes, the class limits in each case being stated and the number of individuals which fall within that particular class being given. Thus, in the class which includes individuals weighing from 110 to 119 pounds there are ten men, the weights of which are 114, 115, 118, 111, 114, 116, 119, 119, 112, and 119 pounds. In the next larger class are thirty-one, and so on. The procedure in making such a classification is to establish arbitrarily the extent and limits of each class and then to check through the whole mass of data, placing each individual in its proper group.

TABLE X.—CLASSIFICATION, FOR WEIGHT, OF THE 200 MEN IN TABLE XVII

Class limits	90–99	100–109	110–119	120–129	130–139	140–149	150–159	160–169	170–179	180–189	190–199
Value of class center (V)............	95	105	115	125	135	145	155	165	175	185	195
Number in each class (f).........	1	2	10	31	54	48	27	14	11	1	1

Thus the first man in Table XVII, whose weight is 135 pounds, would go in the class 130–139; the second, 156 pounds, in the class 150–159, and so through the list. An equally useful classification would result if the class limits were set at a different series of points, such as 145–154, 155–164, and so on. The number of individuals in the various classes will vary slightly, depending on the particular class limits chosen, but this variation is usually negligible. It is important, however, to decide exactly what the limits of each class shall be, so that no confusion may

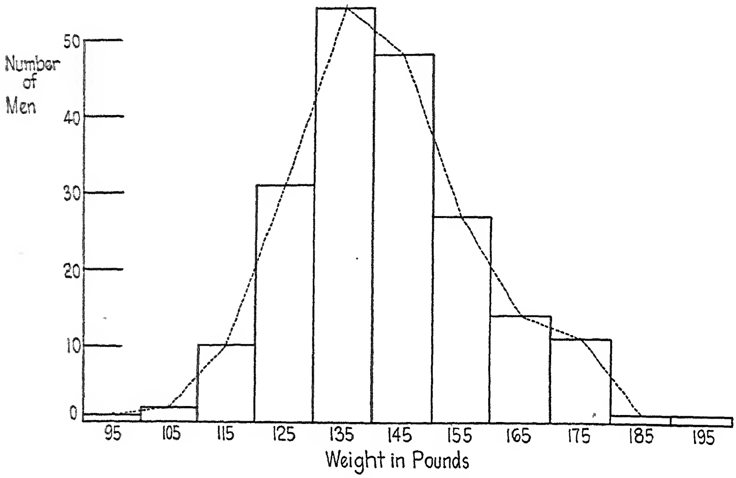


FIG. 82.—Frequency polygon and frequency curve showing variation in weight of 200 college students. A graphic representation of the data in Table X.

arise as to the placing of any individual. In the case here explained the third class, for example, includes all weights from 110 to 119 pounds inclusive. An individual weighing 109 would go in the class below, one weighing 120 in the class above. It is also necessary to determine for each group its *class center*, the value which in later computations is used to stand for the weight of all the individuals in that class.[1] In the case cited it would be 115 pounds.

The Frequency Polygon.—When the original data have thus been classified, it becomes much easier to study the relative frequency of the various weights and so discern the character

[1] The class center is supposed to represent the average value of all the members of the class, and the larger the number in the class, the closer the class center will approximate this value.

of the group as a whole. These facts may be brought out much more vividly, however, if instead of studying the figures alone a graphic representation of them is constructed, the so-called *frequency polygon* or *frequency curve.* If a horizontal line is divided evenly into segments or abscissae representing the number of classes into which the individuals have been grouped, and if upon each of these segments is erected a column the height of which is proportional to the number of individuals in that class, a figure results which presents graphically the composition of the entire group. If the various class centers are united by lines, a frequency curve results. The polygon and the curve representing the body weight of the 200 men here studied are given in Fig. 82 which, it will be seen, is merely the graphic representation of the figures presented in Table X.

The most striking characteristic of this group of individuals is that the various weights are not distributed at all evenly throughout the population, but that there are comparatively few very light men and comparatively few very heavy ones, and that as a point midway between the two extremes is approached the size of the classes progressively increases until it reaches its maximum near the median line of the figure. In other words, the bulk of this population consists of individuals which are intermediate in weight.

The Normal Curve.—Such a curve is found very commonly wherever a group of individuals is classified according to any quantitative character. It tends to approach what mathematicians call the *normal curve* (Fig. 83), a curve representing the relative frequency with which, according to the laws of probability, various consequences may be expected to ensue from the simultaneous action of several independent causes. For example, if six coins were to be tossed simultaneously, the chances of their all falling heads would be very slight and would be expected only once out of $(2)^6$ times, or one time in 64. The chance of throwing five heads and one tail is somewhat greater; of four heads and two tails greater still; and the combination of three heads and three tails is the most likely of all. The chances of two heads and four tails, one head and five tails, and six tails are progressively less and less.[1] The particular combination which appears

[1] The probable chances of each of these combinations, on the basis of 64 throws, corresponds to the coefficients of the various terms in the expansion of the binomial $(a + b)^6$.

in any given case is the result of six independent variables. The chance that they will all tend in the same direction is slight, and it is much more likely that some will tend one way and some another. Plotting the results of the interaction of these causes

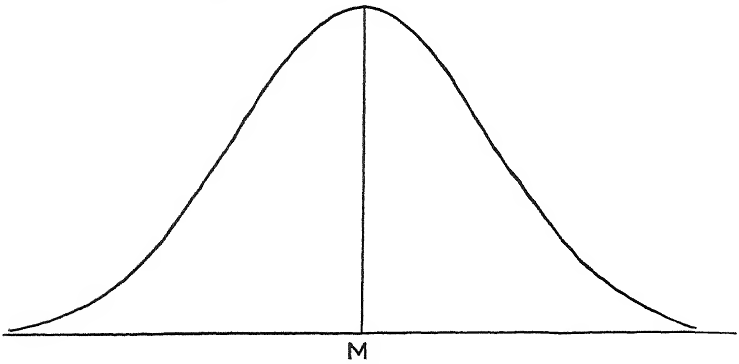


Fig. 83.—A normal curve. The mean and mode are shown by the line at M.

which may be expected on the basis of pure chance, produces a curve approaching the normal one (Fig. 84). That a group of individuals classified for a given quantitative character so commonly shows a curve much like this leads one to suspect

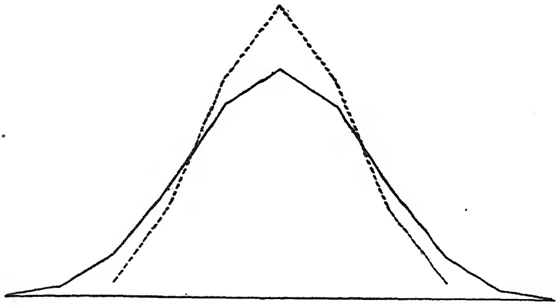


Fig. 84.—Curves representing the expansion of the binomial $(a + b)^6$ (dotted line) and $(a + b)^{10}$ (solid line).

that such characters are affected by a series of factors or influences either in the environment or in the genetic constitution, some of which tend in one direction and some in another, the character resulting from their action usually finding its position at a point intermediate between the two possible extremes.

By no means all groups of individuals, however, which are classified or plotted for a given size character will show a rela-

tively smooth and regular curve. In many instances the figure may be unsymmetrical, with a steep slope on one side and a gradual one on the other, a so-called *skew* curve; or it may be still more complex and present two (or even more) distinct peaks or modes, thus forming a bimodal or multimodal curve (Fig. 85). Such a curve may indicate a mixture of types, segregation of genetic factors, unequal environmental influences, or other disturbing causes. In the majority of cases, however, there is at least an approach to a symmetrical curve, high in the middle (the intermediate classes) and falling away toward each end

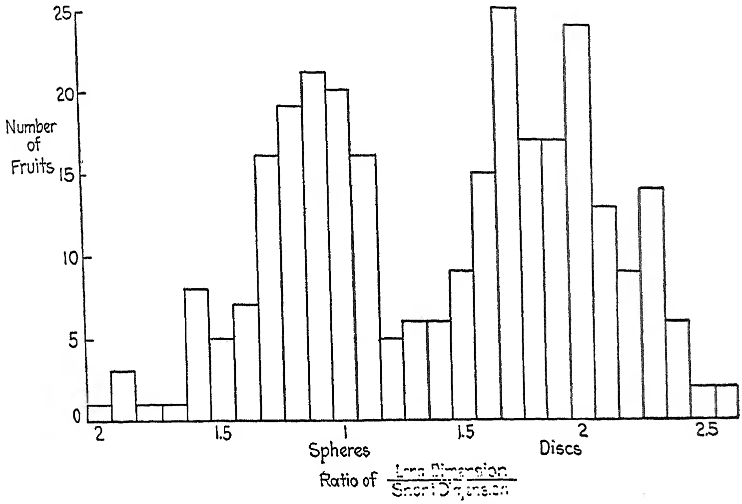


FIG. 85.—A bimodal frequency polygon showing variation in the shape of fruits of the summer squash. The left-hand group contains spherical fruits, with an index of about 1.0; the right-hand group contains flat or disc-shaped fruits, with an index of about 2.0. The bimodal polygon here indicates segregation in F_2 of two complementary factors for fruit shape in a ratio of 9:7.

The division of a mass of data into classes and the plotting of these classes in a polygon or curve helps greatly in presenting a simple picture of the size relations of a given group, but it is still far from providing the two determinations which are sought —a quantity which shall stand for the group as a whole, and another which shall measure the variation within the group. These two constants must be derived from a study of the classified data.

The Mode.—In an ordinary curve there is usually one class, commonly situated about midway between the two extremes,

which contains more individuals than do any of the others. This is known as the modal class or the *mode*. For the group of men studied, the class from 130 to 139 pounds (Fig. 82) is the mode. Since the mode is the most populous and "fashionable" of all the classes, it may be taken as a rough indication of the *type* of the population as a whole. If a single individual were to be selected as typical of the group, it would probably be chosen from among the members of the modal class.

The Mean.—The mode, however, is often considerably nearer one extreme than the other, and there also may be two or more classes of equal or almost equal size, so that as a quantity which shall represent the group as a whole the mode is not satisfactory. The figure which best serves this purpose is the arithmetical average, or *mean*. This constant may, of course, be obtained by adding the values for all the individuals and dividing this by the total number. A simpler method, and one substantially as accurate, is to classify the individuals (as has already been done for the group of men under consideration) and then to multiply the value of each class by the number within it, add these products, and divide by the total number of individuals. The value (class center) which is used to stand for the entire class is that halfway between the two extremes which the class includes, and in the weight classes which have been used falls at 105 pounds, 115 pounds, 125 pounds, and so on. M is commonly employed to denote the mean, V the value of a given class center, f the number of individuals in a class (the class frequency), and n the total number of individuals. Σ is the mathematical symbol for summation. Thus

$$M = \frac{\Sigma fV}{n}.$$

In determining these biometrical constants the classes are arranged in a vertical, rather than horizontal column, as in the plotted curve. In Table XI the class centers of the group of men being studied, for weight, are thus placed under V with the corresponding number of individuals at the right of each class center, under f. The third column (fV) contains the products of each class value by its class frequency. Using the formula given above, the mean is

$$\frac{28{,}380}{200} = 141.9 \text{ pounds.}^{1}$$

[1] A simpler method of determining the mean will be explained later.

This is the average weight of the group under consideration and gives important information as to this particular trait in these individuals. The mean often lies within the modal class but in an asymmetrical curve may be far on either side of the mode.

TABLE XI.—THE DETERMINATION ON THE MEAN (LONG METHOD)

V	f	fV
95	1	95
105	2	210
115	10	1,150
125	31	3,875
135	54	7,290
145	48	6,960
155	27	4,185
165	14	2,310
175	11	1,925
185	1	185
195	1	195
	200	28,380

$$M = \frac{fV}{n} = \frac{28,380}{200} = 141.90 \text{ pounds.}$$

The Average Deviation.—More difficult to arrive at is a measure of variation. Two populations may have the same mean but

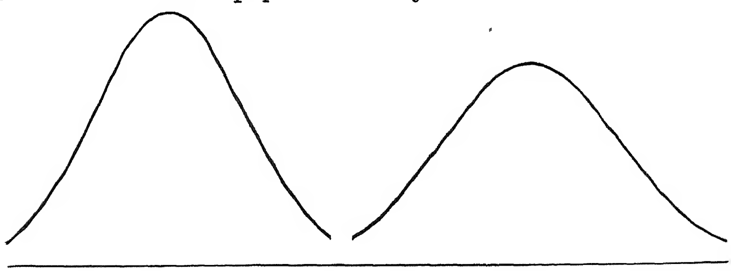


FIG. 86.—Differences in variability indicated graphically. At left a curve representing a population of comparatively low variability. At right, one representing a population of the same size but greater variability. (*After Babcock and Clausen.*)

may differ markedly in their variability. In one, the individuals may be grouped in a fairly compact body, with the extremes not far apart, and in the other they may be dispersed over a much greater distance. Two frequency curves, one with high and one with low variability, are shown in Fig. 86. An inspection of

the frequency curve will give a general idea of this degree of variability, but to measure this requires, first the establishment of a definite point with reference to which variation can be determined; and, second, a measurement of the deviation of each individual from this point. The mean is the most obvious point from which to measure variation. Once this has been established it is a simple matter to determine the deviation of each individual (or class) from this mean and thus to arrive at the *average* amount of deviation displayed by the population as a whole. Letting d represent the deviation of an individual or class from the mean, the *average deviation* will be $\frac{\Sigma fd}{n}$. This quantity may be used as an approximate measure of variation. In Table XII, the V and f columns are as before, but there have been added the columns d, giving the deviation of each class from the mean, and fd, the product of the deviation of each class by the number of individuals in it. The sum of the column fd divided by the total number of individuals will thus give us the average deviation from the mean. This will be, in the example, $\frac{2{,}572.4}{200}$, or 12.86 pounds.

TABLE XII.—THE DETERMINATION OF THE AVERAGE DEVIATION AND THE STANDARD DEVIATION (LONG METHOD)

V	f	d	fd	fd^2
95	1	46.9	46.9	2,199.61
105	2	36.9	73.8	2,723.22
115	10	26.9	269.0	7,236.10
125	31	16.9	523.9	8,853.91
135	54	6.9	372.6	2,570.94
145	48	3.1	148.8	461.28
155	27	13.1	353.7	4,633.47
165	14	23.1	323.4	7,470.54
175	11	33.1	364.1	12,051.71
185	1	43.1	43.1	1,857.61
195	1	53.1	53.1	2,819.61
	200		2,572.4	52,870.00

$$\text{Average deviation} = \frac{\Sigma fd}{n} = \frac{2{,}572.4}{200} = 12.86 \text{ pounds.}$$

$$\sigma = \sqrt{\frac{\Sigma fd^2}{n}} = \sqrt{\frac{52{,}870}{200}} = \sqrt{264.35} = 16.26 \text{ pounds.}$$

The Standard Deviation.—A more accurate method of measuring variation, however, is to *square* the deviations and then extract the square root of their sum. The reason may be made clear by the familiar example of shooting at a target. A shot to be 6 inches from the bull's eye, must be somewhere within a total area of approximately 1 square foot. If the deviation from the bull's eye is twice as great, or 1 foot, the total area within which the shot may lie is not twice as great as before but the square of twice, or four times as great, since the area within a foot's radius of the center is approximately 4 square feet. Thus it is four times as hard to get within 6 inches of the bull's eye as it is to get within a foot of it; and in comparing the rifle score of two persons (their "variability" in marksmanship) it is evidently fairer to square the distance of each shot, average these squared values and then extract the square root of this average, than to average the actual distances themselves. This is the method commonly followed in biometry and the resulting constant is known as the *standard deviation*, σ, its formula being $\sqrt{\frac{\Sigma fd^2}{n}}$.

To obtain this it is necessary to add another column to the table, that of the squared deviation of each class multiplied by its class frequency, or fd^2. This may, obviously, be obtained by multiplying the d and fd columns, and such a column has been added to Table XII. The standard deviation in the example is thus $\sqrt{\frac{52,870}{200}}$, or 16.26 pounds.

The Short Method.—The determination of mean and standard deviation in this way usually involves, as here, complex fractional values and much arduous calculation. A much simpler method has been devised which is just as accurate and which avoids the use of fractions (Table XIII). This method, briefly, is to *assume* that the mean falls on an even class value, to measure the standard deviations from this *assumed* mean, a, and then to make the necessary correction. In the problem at hand, assume that the mean weight is exactly 135 pounds. From this assumed mean the deviations of the various classes (here commonly represented by d') are determined. Care must be taken to distinguish those which are *plus* in sign (deviations of classes with a greater class value than a) from those with a *minus* sign. It is simpler to treat the deviations as unit quantities (+1, +2, +3, −1, −2, −3, and so on) rather than to express them in terms of the actual measurements used, which in the example

would be +10, +20, +30 *pounds*. This avoids the use of large numbers, and the results thus obtained can readily be converted into terms of the units of measurement employed by multiplying them by the true class interval i, which in this example is 10.

TABLE XIII.—THE DETERMINATION OF THE MEAN, STANDARD DEVIATION, AND COEFFICIENT OF VARIABILITY BY THE SHORT METHOD

V	f	d'	fd'	fd'^2
95	1	−4	− 4	16
105	2	−3	− 6	18
115	10	−2	− 20	40
125	31	−1	− 31	31
135	54	0	0	0
145	48	+1	48	48
155	27	+2	54	108
165	14	+3	42	126
175	11	+4	44	176
185	1	+5	5	25
195	1	+6	6	36
	200		+138	624

a = 135 pounds.
i = 10.

$$c = \frac{\Sigma fd'}{n} = \frac{+138}{200} = +0.69 \text{ pounds.}$$

$$M = a + (c \times i) = 135 + (+0.69 \times 10) = 141.90 \text{ pounds.}$$

$$\sigma = \sqrt{\frac{\Sigma fd'^2}{n} - (c)^2} \times i = \sqrt{\frac{624}{200} - (+0.69)^2} \times 10 = 16.26 \text{ pounds.}$$

$$C.V. = \frac{\sigma \times 100}{M} = \frac{16.26 \times 100}{141.90} = 11.46 \text{ per cent.}$$

The d', fd', and fd'^2 columns are then obtained much more easily than by the long method. If the assumed mean should happen to fall exactly on the true one, the sum of all the deviations plus and minus (the sum of the fd' column) would be zero. If the assumed mean is less than the true one, however, the sum of the deviations will be a *plus* quantity, and if greater, a *minus* quantity. If this sum is divided by the total number of individuals the *correction*, c, is obtained which, if added to or subtracted from the assumed mean (according as the sign is plus or minus) will give the true mean. The formula for the correction is thus $\frac{\Sigma fd'}{n}$, which in the example is $\frac{+138}{200}$ or + 0.69. This multiplied by the class interval i gives 6.9 pounds, which added to the assumed mean, 135 pounds, gives the true mean, 141.90 pounds,

exactly the figure arrived at by the long method. The formula for the mean by the short method is thus $a + (c \times i)$.[1]

The use of the assumed mean and the correction thus gives us an easy way of determining the mean, but it is equally valuable in determining the standard deviation. If, from the average squared deviations from the assumed mean, the square of the correction is subtracted before the square root of the whole is finally extracted, the true standard deviation will be obtained. The formula for the standard deviation by the short method is thus $\sqrt{\frac{\Sigma fd'^2}{n} - c^2} \times i$. The method for the determination of the mean and standard deviation by the short method is set forth in the Table XIII. The standard deviation in this case would thus be $\sqrt{\frac{624}{200} - 0.476} \times 10$, or 16.26 pounds, exactly the result obtained by the long method.

The Coefficient of Variability.—The standard deviation is, of course, always in terms of the units used (pounds in our example) and its usefulness lies in comparing the variability of groups of individuals with regard to the same character. It is often necessary, however, to compare variability in one character with variability in another—for example, the variation in the weight of the men studied with the variation in their height—and for that purpose the standard deviation is useless, since pounds and inches cannot be compared. To avoid this difficulty the *coefficient of variability*, *C. V.*, is employed which is merely the standard deviation divided by the mean and expressed as per cent, its formula being $\frac{\sigma \times 100}{M}$, which in the example is $\frac{1,626}{141.90}$, or 11.46 per cent.

The formulas for the mean, correction, standard deviation, and coefficient of variability, as determined by the short method, are brought together below:

$$a = \text{assumed mean.}$$

$$M = a + (c \times i).$$

$$c = \frac{\Sigma fd'}{n}.$$

$$\sigma = \sqrt{\frac{\Sigma fd'^2}{n} - (c)^2} \times i.$$

$$C.\ V. = \frac{\sigma \times 100}{M}.$$

[1] In all these formulas, if $i = 1$, it obviously may be neglected.

The Probable Error.—Of course, the value and the reliability of the figures thus obtained depend to a large extent on the number of individuals studied—the larger the number the more trustworthy the figures. We could determine the mean, standard deviation and coefficient of variability of body weight for fifty men chosen at random from the student body of a college, but constants derived from this small sample would be much less likely to give a correct idea of the college population as a whole than ones based on 500 men. For this reason any biometrical constants, such as those just worked out for body weight, should be followed by some measure of reliability, usually a fractional figure technically known as the *probable error* and preceded by a "plus or minus" sign, $\pm$. The mathematics involved in the derivation of this figure need not be discussed here, but the student should understand clearly what the probable error tells about the quantity or constant to which it is appended: namely, that if it is added to and subtracted from the constant, the two resulting figures are the limits between which *there is an even chance* that the true value lies. The probable error of the mean in the example is ± 0.775 pounds, which means that another sample from the same population would have a mean, at least every other time, which would lie between 142.675 and 141.125 pounds. Where the probable error is large, these limits are wide and it is correspondingly uncertain as to how close the figure (which is based on a relatively small sample) is to the true value for the entire population from which the sample was drawn. If the probable error is small, the probability that the figure approaches the truth is greater. The formulas for the probable error of the mean, standard deviation and coefficient of variability are given below:

$$E_M = 0.6745 \frac{\sigma}{\sqrt{n}}.$$

$$E\sigma = 0.6745 \frac{\sigma}{\sqrt{2n}}.$$

$$E_{C.\,V.} = 0.6745 \frac{C.\,V.}{\sqrt{2n}}.$$

The constants for the group of men studied, as to body weight, should, therefore, be written as follows:

$$M = 141.90 \pm 0.775 \text{ pounds.}$$

$$\sigma = 16.26 \pm 0.548 \text{ pounds.}$$

$$C.\,V. = 11.46 \pm 0.386 \text{ per cent.}$$

The Inheritance of Quantitative Characters.—These methods of biometrical analysis were applied by Francis Galton in his studies of such quantitative traits as height in man. Through these studies he was led to enrich the science of inheritance by the development of valuable statistical methods, and to burden it with a conception of inheritance, the inadequacy of which has clearly been shown by the mendelian interpretation of heredity.

Galton's "Law."—Galton's interpretation of quantitative inheritance was called by him the *law of ancestral heredity.* He derived it chiefly from data on human stature which, as seen above, is apparently a complex trait, showing continuous variation. From comparisons of the average statures of progeny with the averages of the parents and of remote ancestors, and from measurements of the degree of resemblance between parents and offspring by means of the correlation method (page 260) which he devised, Galton concluded that, although the offspring inherited their stature chiefly from the parents, they were also influenced by the remoter ancestors. In general, he thought that the remoter the ancestor the less influence it exerted on the characters of the descendant. He stated this law of ancestral heredity as follows:

> The two parents contribute between them on the average one-half (0.5); the four grand-parents one-quarter $(0.5)^2$; the eight great grand-parents one-eighth $(0.5)^3$ etc. Thus the sum of the ancestral contributions is expressed by the series (0.5)-$(0.5)^2$-$(0.5)^3$ which, being equal to one, accounts for the whole heritage.

This law has been widely applied to quantitative characters, and does provide a good *description* of the inheritance of such variable traits. But that it does not provide an *explanation* of inheritance becomes evident when one remembers that it assumes that the inheritance is infinitely divisible, whereas mendelian data show that inheritance, in general, is not thus divisible but is organized into discrete indivisible entities, the genes. It fails to account for the most general feature of inheritance—the sharp segregation of single genes which do not blend but show strictly alternative inheritance. For these reasons, Galton's law can no longer be regarded as applicable to any traits, either in man, animals, or plants.

Biometrical Analysis of Quantitative Inheritance.—The same biometric methods, however, have been of great value in modern studies of quantitative inheritance. They will now be applied

to a concrete case of the inheritance of a size character, that of ear length in corn, as studied by East. He worked with two relatively pure types of corn; one, long-eared Black Mexican

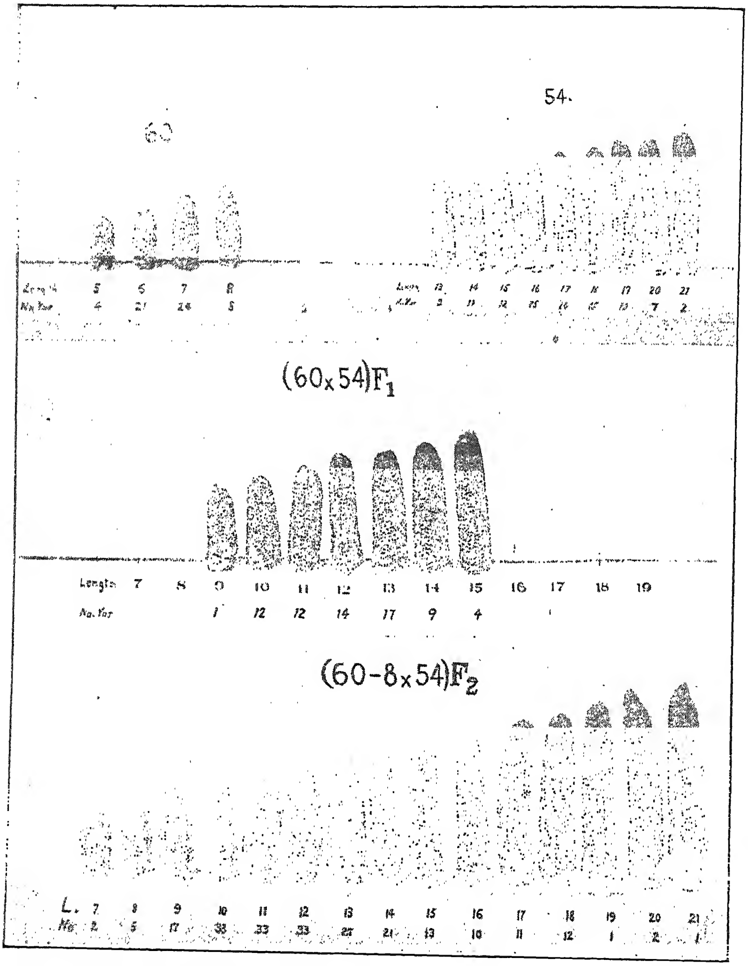


FIG. 87.—The inheritance of ear length in corn, as shown by the results of crossing a short-eared variety of popcorn with a long-eared variety of sweet corn. Ears showing the range in length of the parent types are pictured above, with the F_1 and F_2 generations below. (*From East.*)

sweet, and the other, short-eared Tom Thumb pop (Fig. 87). In Table XIV are classified, in 1-centimeter classes, the 54 individuals of the pop race studied, the 101 individuals of the Black Mexican

race, the 69 individuals of the F_1 raised from a cross between these two, and the 221 individuals of the F_2 obtained by crossing F_1 plants. The mean, standard deviation and coefficient of variability for each of these four groups are also presented.

It will be noted that even in the pure types the individuals vary somewhat in ear length, but these differences are presumably due to environmental conditions, which are very hard to equalize exactly. The mean ear length for each race, however, rather than the length of any one group of individuals may be taken as representative of the race as a whole. The means of the parent types differ by 10.2 centimeters. The variability of these two types, however, is low and of about the same magnitude. There are two noteworthy facts about the F_1: first, that its mean is approximately intermediate between that of the two parents (12.1 as compared with 6.6 and 16.8); and, second, that its variability is about as low as theirs (12.48 as compared with 12.27 and 11.13). The F_2 is still different. Its mean is very close to that of the F_1, but *its variability has increased very greatly*, rising to 22.30 per cent. Some plants are found in this generation with ears as long as the mean of the sweet type and some with ears as short as that of the pop type, with others ranging all the way between.

TABLE XIV.—FREQUENCY DISTRIBUTION OF LENGTHS OF EARS IN CROSS OF LONG-EARED (60) AND SHORT-EARED (54) CORN. (*From East*)

Line number	Class centers in centimeters for lengths of ears																	M	σ	$C.V.$
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21			
60	4	21	24	8	..	..	..	..	..	..	..	..	..	..	..	..	..	6.6 ± 0.07	0.81 ± 0.05	12.27 ± 0.78
54	..	..	..	..	..	..	..	..	3	11	12	15	26	15	10	7	2	16.8 ± 0.12	1.87 ± 0.09	11.13 ± 0.53
$(60 \times 54)F_1$	..	..	..	..	1	12	12	14	17	9	4	..	..	..	..	..	..	12.1 ± 0.12	1.51 ± 0.09	12.48 ± 0.72
$(60 \times 54)F_2$	..	..	2	5	17	33	33	33	27	21	13	10	11	12	1	2	1	12.6 ± 0.13	2.81 ± 0.09	22.30 ± 0.74

The Multiple Factor Hypothesis.—This example is typical of most of the cases where the inheritance of a size character has been carefully worked out. What does it indicate as to the method by which such traits are transmitted? Are they really outside the operation of Mendel's laws, as was long supposed, or is it possible to reconcile their behavior with the fundamental principles of mendelism?

In the first place, dominance is clearly lacking and the inheritance is of the "blending" type, the F_1 mean being intermediate between the two parental ones. A few size characters are known

which show dominance (such as vine height in peas as studied by Mendel himself), but the great majority of them certainly do not (Fig. 81).

Of more significance is the sharp rise in variability between the F_1 and the F_2, and the reappearance in the latter generation of both parental types. This at once suggests the segregation of genetic factors. Consider, for example, what happens when a homozygous dilute, cinnamon, unspotted mouse is crossed with a homozygous pink-eyed spotted black one. The F_1 mice are all wild gray and show no more variability than does either homozygous parent. The F_2, however, is extremely variable, giving thirty-two kinds of visibily different types, including animals like either grandparent. Coat color in mice is evidently determined not by one but by a considerable number of factors, each different in its effect, and this F_2 variability is due to their independent segregation. In this case each factor affects a different quality—one the banding of the hairs, another the development of black as distinguished from brown in the hair, and so on. If we assume that in determining a given size character there are likewise a considerable number of independent factors (lacking dominance), but that each, instead of having a specific effect, visibly different from the rest, affects the *same* character, in this case size, and is cumulative in its influence and merely adds a certain amount to the particular size character (or subtracts a certain amount therefrom), then the results obtained in the inheritance of size are readily explainable. That most quantitative characters are controlled by a series of similar but independent and cumulative factors is the explanation which the *multiple-factor* hypothesis offers for the inheritance of such traits.

Analogy from Duplicate Factors.—Before discussing this hypothesis more fully, it will be well to inquire what evidence there is, aside from that derived through a biometrical analysis of parents, F_1 and F_2, that a quantitative character is indeed controlled by a series of such multiple factors. In an earlier chapter (page 106) the operation of *duplicate* factors, such as those discovered by Shull for capsule shape in *Bursa*, has been described. Here there are two factors for triangular capsules, each dominant over one for cylindrical shape, and either alone sufficient to produce the triangular effect. A cross between a plant homozygous for both of them (AA BB) and a plant with

cylindrical pods (*aa bb*) produces a triangular F_1 (*Aa Bb*); and of the F_2, fifteen-sixteenths are triangular and only one-sixteenth cylindrical (Fig. 41, page 107). Here are two factors affecting the same character and indistinguishable, though not cumulative, in their effect.

Somewhat similar is the case of the inheritance of colored grains in wheat investigated by Nilsson-Ehle and described above (page 108), which led to the formulation by him of the multiple-factor hypothesis. Here also there are evidently two independent factors for red, but of more significance is the fact that the F_1 plants are much paler in color than their red parents, and that among the F_2 red plants there are a few which are as dark red as the red grandparent, a considerable number which are of about the same shade as the F_1, and some which are even paler than the F_1. The conclusion seems obvious (and is supported by a study of F_3 generations raised from these various types) that there are here two pairs of factors for red, neither completely dominant over white and either capable of producing red kernels; but that the four members of these pairs are cumulative in their effect, the dark reds being due to the presence of four factors, the next in intensity to three, those like the F_1 to two, and the pale reds to but one. Representing one of these factor-pairs by *AA* and the other by *BB*, the original dark red parent is *AA BB* and the white one *aa bb*. The F_1 is *Aa Bb*, intermediate in color. The checkerboard (Fig. 42, page 109) shows the genotypes of the F_2 plants, with the number of red factors possessed by each class. Only one of the fifteen reds has all four factors, and is thus dark red; four have three factors, six have two, four have one, and one-sixteenth of the whole population has none.

In the case reported by Nilsson-Ehle involving three factor-pairs (page 108), the same difference in intensity of coloration among the F_2 red plants was found, there being few that were dark, many that were intermediate, and few light. If in this case it is assumed that there are three independent factors for red, the red parent may be represented as *AA BB CC*, the white as *aa bb cc*, and the F_1 as *Aa Bb Cc*. In Fig. 88 are plotted, in the form of a frequency polygon, the F_2 individuals having six, five, four, three, two, one, and no red factors respectively. It will be noted that the mean of the F_2 is like that of the F_1 (possessing three factors), but that instead of having the constancy of

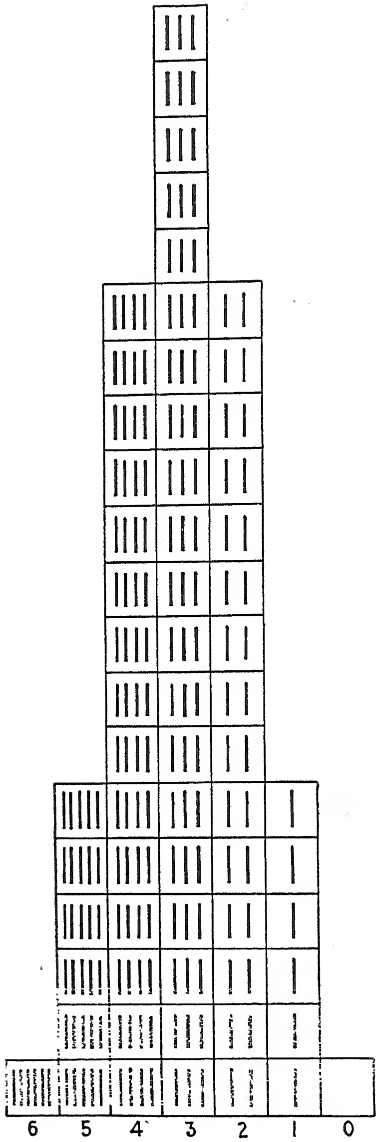


Fig. 88.—Diagram illustrating the frequency of the seven kinds of factor combinations possible in F_2 from a cross of parents differing in three pairs of duplicate or cumulative factors, such as those for red kernel color in wheat (*AA BB CC* × *aa bb cc*).

the F_1, this generation is very variable and includes plants ranging all the way from one grandparental type to the other.

Red kernel color here behaves essentially like an ordinary quantitative character. If, instead of an additional unit of redness, each factor should contribute a unit of height, weight, or other quantitative trait, the resulting parental, F_1 and F_2 generations would appear as we find them, except for the additional variation produced by environmental influences. Assume, for example, that the mean weight of a light race of poultry is 3 pounds and that of a heavy one 6 pounds, and that this difference is caused by three independent pairs of factors, the 3-pound race being represented by *aa bb cc* and the 6-pound one by *AA BB CC*, none of the factors showing dominance, all of them being equal, and each adding half a pound to body weight. The F_1 would be *Aa Bb Cc* and would thus weigh 4½ pounds; and the F_2 would have a distribution like that of the grades of red color as shown in Fig. 88, one sixty-fourth weighing 6, six sixty-fourths 5½, fifteen sixty-fourths 5, twenty sixty-fourths 4½, fifteen sixty-fourths 4, six sixty-fourths, 3½, and one sixty-fourth 3 pounds. The coefficient of variability of this F_2, due to segregation of genetic factors alone, would be 30.6 per cent. Such a situation is not far from what probably occurs in the inheritance of body weight in poultry.

If three factor-pairs are responsible for a given size difference, as assumed in the previous example, it is evident that an individual as extreme as one of the grandparental types may be expected to appear only about once in sixty-four times. In the inheritance of most quantitative characters, however, the original types are recovered in the F_2 much less frequently than this, and it is therefore inferred that more than three factor-pairs are involved. A rough guess as to their number can be made by determining the proportion of the F_2 which resembles one of the P_1 types. If three factor-pairs are concerned, the parental type will reappear in approximately 1/64 of the individuals; if four, in about 1/256; if five, in about 1/1,024; if six, in about 1/4,096; and so on. If the number of factors is large, individuals like the grandparents will not appear in a small F_2 (as often happens). In the inheritance of corn ear length, for example, as shown in Table XIV, there are evidently few factors involved in the difference between the sweet and the pop types. In Table XV, for corolla length in tobacco (Fig. 89), however, there seem

to be more than this, for in a rather large F_2 the parent types do not reappear at all.

The fact that quantitative traits are apparently due to a series of independent factors will evidently result in differences in breeding behavior between individuals which are similar in appearance. Two animals, for example, may have the same weight but one may owe it to one group of factors and the other to factors of the same number but which belong to different

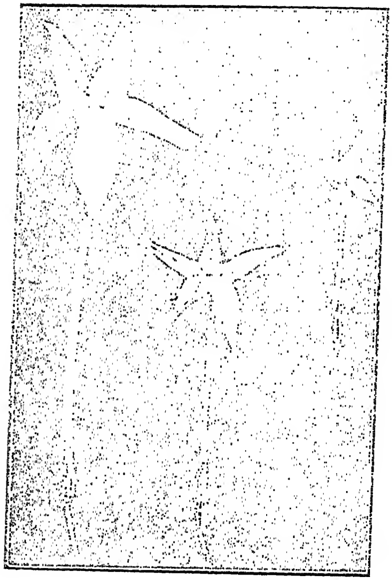


FIG. 89.—Flowers showing the average corolla length of two varieties of *Nicotiana longiflora* (left and right) and an average flower from the F_2 of a cross between them (center). (*From East.*)

factor pairs, with a consequent recombination of factors in the offspring of a cross between them Two others may have the same weight, but one may owe it to factors all of which are in a homozygous condition and the other to the same number of factors, some or all of which may be in a heterozygous condition. The former will breed essentially true to its weight, but the latter will show a considerable amount of variation due to the segregation of factors. The results obtained from crosses involving quantitative characters and the efficacy of selection in producing permanent changes of type will thus depend on the particular

factors possessed by the individuals concerned and on the manner in which these factors are distributed in the genotype.

TABLE XV.—FREQUENCY DISTRIBUTIONS FOR COROLLA LENGTH IN A CROSS BETWEEN VARIETIES OF *Nicotiana Longiflora Cav.* (*from East*)

Variety Number	Year	Class centers in millimeters																							
		34	37	40	43	46	49	52	55	58	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
P_1 383	1911	..	13	80	32																				
P_1 383	1912	1	4	28	16																				
P_1 383	1913	..	4	32	1																				
P_1 330	1911	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6	22	49	11	
P_1 330	1912	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	16	32	6	1
P_1 330	1913	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	7	10	2	
F_1 383 × 330	1911	..	..	..	..	..	..	..	4	10	41	75	40	3											
F_2 383 × 330	1912	..	..	..	..	..	..	1	5	16	23	18	62	37	25	16	4	2	2						

Differences among Multiple Factors in Effect and Location.—The same quantitative trait, in the same series of individuals, is not always controlled by the same number of factors, nor have

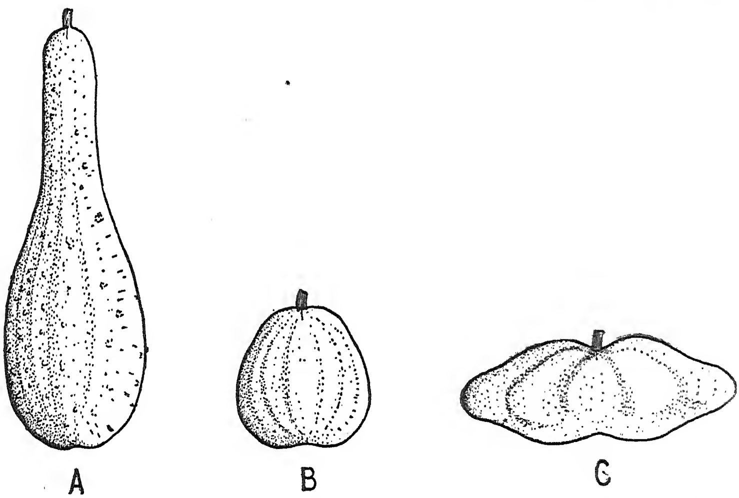


FIG. 90.—Three true-breeding shape types of summer squash. A, long; B, sphere; C, disc.

all these factors the same effect. Sometimes a difference may be found which is evidently due to one factor, and, in the same material, differences of the same sort may appear in which several factors are clearly involved. This is well shown in the inheritance

of fruit shape in summer squashes (Fig. 90), a quantitative character represented by the ratio or index between the long and short dimensions of the fruit. The difference between a disc type and

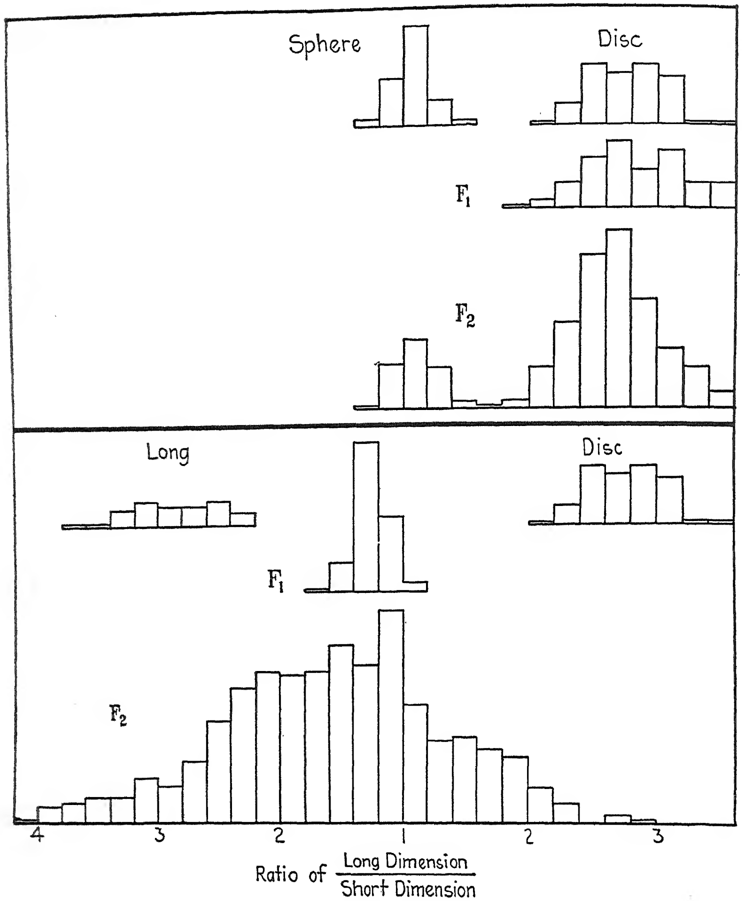


FIG. 91.—Inheritance of fruit shape in summer squashes. Upper figure; results of a cross between sphere and disc squashes (Fig. 90) showing dominance and segregation of a single shape factor. Lower figure: results of a cross between a long and a disc squash, showing absence of dominance and segregation of many shape factors in F_2.

a sphere is clearly due to one factor-pair, as indicated by the distribution of individuals in the parental, F_1 and F_2 generations as shown in Fig. 91, for there is a clean-cut segregation in F_2 into approximately three-fourths disc and one-fourth sphere

plants. In the cross of the same disc with a long type, however, several factors are evidently involved, since the F_2 shows a rather smooth curve with no very evident segregation (Fig. 91).

It will be noted: (1) that essentially the same degree of difference in shape is produced by one factor as by several, indicating that these multiple factors are not all alike but differ in the intensity of their effects; and (2) that one shows dominance and the others do not. There is reason to believe that in other cases quantitative factors differ in the degree of their effects and in dominance, and thus complicate the problem of the inheritance of quantitative traits. It must be admitted, too, that the evidence which has thus far been presented for the multiple-factor hypothesis is wholly inferential. Conclusive proof that such factors actually exist will be furnished only when we are able to isolate them and study their individual effect just as we do for those which determine other characters.

A beginning has actually been made at this difficult task, through a study of the linkage relations between size factors and those which control certain qualitative characters. Sax, for example, has found that in beans there is a factor which increases seed weight by five or six centigrams and is linked with the factor for the pigmentation of the seed coat; and Lindstrom has found one which increases the fruit weight of tomatoes and is linked with yellow skin color. More illuminating, however, is the work of Warren on egg size in *Drosophila.* This material is especially favorable because of the readily determined linkage relations and the large number of other characters known. Warren found egg length to differ markedly in various mutant races and to be relatively free from influence by the size and age of the female or by temperature differences. He was able to determine the existence of factors for egg size in all four linkage groups; to prove that they differed in the intensity of their effect, and that they behaved in inheritance like ordinary factors, segregating purely, showing independent assortment with those size and other factors which occurred in different chromosomes, and linkage with those which occurred in the same chromosome. This is the first case in which a series of size factors has been definitely located in the chromosomes.

All the facts at hand, therefore, seem to lend support to the multiple-factor hypothesis of size inheritance, and it is certainly the most satisfactory explanation yet put forward for the

characteristic method of inheritance of quantitative traits which was long a puzzle to geneticists. Its chief contribution has consisted in bringing size characters, at first thought to be radically different in their inheritance from qualitative ones, definitely under the operation of mendelian principles.

APPENDIX

The Measurement of Correlation.—In studies of variation a difference in one trait is often found associated with a difference in another, these variations being spoken of as *correlated* with one another. Thus Mendel found that pea plants in which the seed coats were gray always bore purple flowers and that those in which they were white, bore white flowers. In the same way, albino rodents have pink eyes and those with pigmented coats have pigmented eyes. Between these traits correlation is perfect, but where quantitative characters are concerned such absolute correspondence is rarely found between the degree of development of one trait and that of another. Thus, in general, the taller a man is, the more he will weigh, but the correlation between these two characters obviously is not perfect, since there are many individuals who are relatively tall and thin, and others who are relatively short and stout; so that for every added inch in height there is not always a definite and proportional increase in weight.

Among correlated quantitative traits all degrees in the intensity of their correlation with each other are found, and some method is, therefore, needed for measuring the *degree of correlation.* This will prove useful not only in studying the relationship of two different traits but also in determining, for a single trait, the degree of resemblance between parent and offspring by correlating members of the two generations with each other in respect to this character, as did Galton in his studies of stature. Such a method of measuring correlation was devised by Galton and has been perfected by later biometricians. It consists in determining the *coefficient of correlation,* a quantity usually designated by r; and as this method is of especial usefulness in the solution of certain problems of genetics (and is also being widely employed in other fields of science) it will be briefly described here.

In determining the degree of correlation between two characters a number of individuals (the more the better, of course) are each measured for the two characters in question. To find a correlation between weight and height in man, for example, the same group of 200 men may be studied whose weights were analyzed in this chapter, and not only the weight but also the height of each determined. These figures are presented in Table XVII below. These men may now be arranged in groups as to height, and the curve may be plotted for height as it was for weight, but these curves will tell nothing about the relationship between the two characters. To find this, every individual must be plotted with reference to *both traits at once* and the data must be arranged in the form of a *correlation table* (Table XVI). Here the two classifications are superimposed on one another, and each man is placed in his proper class with reference to both. Thus the first man on the list, who weighs 135 pounds and is 67 inches tall belongs in the class including

individuals weighing from 130–139 pounds; and, in the array at right angles to this, in the group of 67-inch men. In this way every individual is entered in the square at the intersection of the two class rows where he belongs, and when all have been so disposed of, the individuals in each square are counted, and the number of the total placed in the square. This has already been done in Table XVI.

TABLE XVI.—DETERMINATION OF THE COEFFICIENT OF CORRELATION, r, BETWEEN WEIGHT AND HEIGHT FOR THE 200 MEN IN TABLE XVII

Height (y) in inches $a = 68.5$; Weight (x) in Pounds $a = 135$

V	58–59 (58.5)	60–61 (60.5)	62–63 (62.5)	64–65 (64.5)	66–67 (66.5)	68–69 (68.5)	70–71 (70.5)	72–73 (72.5)	74–75 (74.5)	f	d'	fd'	fd'^2	ΣP
90– 99 (95)			[illegible]							[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
100–109 (105)			[illegible]							[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
110–119 (115)			[illegible]	[illegible]	[illegible]					[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
120–129 (125)		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
130–139 (135)		1	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		[illegible]		[illegible]	[illegible]	[illegible]
140–149 (145)	[illegible]			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
150–159 (155)					[illegible]	[illegible]	[illegible]	[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
160–169 (165)					[illegible]	[illegible]	[illegible]	[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
170–179 (175)					[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
180–189 (185)									[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
190–199 (195)							[illegible]			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
f	1	2	7	31	59	60	24	14	2	200		+138	624	180
d'	−5	−4	− 3	− 2	− 1	0	1	2	3					
fd'	−5	−8	−21	−62	−59	0	24	28	6	−97				
fd'^2	25	32	63	124	59	0	24	56	18	401				

Weight (x)

$$c_x = \frac{+138}{200} = +0.69$$

$$\sigma_x = \sqrt{\frac{624}{200} - (+0.69)^2} = 1.626$$

Height (y)

$$c_y = \frac{-97}{200} = -0.49$$

$$\sigma_y = \sqrt{\frac{401}{200} - (-0.49)^2} = 1.330$$

$$r_{xy} = \frac{\frac{\Sigma P}{n} - (c_x\,c_y)}{\sigma_x\,\sigma_y} = \frac{\frac{180}{200} - (+0.69 \times -0.49)}{1.626 \times 1.330} = +0.571$$

$$Er = \frac{0.6745(1 - r^2)}{\sqrt{n}} = \frac{0.4545}{14.14} = \pm 0.032$$

$$r_{xy} = +0.571 \pm 0.032$$

To solve the formula for the coefficient of correlation it is necessary to determine the correction and the standard deviation for each variable, and these are arrived at in the ordinary way by the use of the short method. Thus for weight the f', d', fd', and fd'^2 columns are arranged as before. For height the same is done as for weight, except that the columns are arranged at right angles to the other series but in the same order with reference to the table. Analysis of these figures gives a correction and a standard deviation for weight (as before but uncorrected) of $+0.69$ and 1.626; and for height of -0.49 and 1.330, respectively.

In addition to these another quantity must now be determined, the sum of the deviations of every individual from one (assumed) mean multiplied by its deviation from the other mean. This is obtained by summating the column headed ΣP (sum of products). In this column is entered the number of individuals in each square multiplied by the product of the deviation of that square from *both* assumed means, care being taken in every case to regard the signs of the quantities involved. The sum for all the squares in one horizontal row must first be brought together and entered under the ΣP column at the end of this row, and then these entries must be added. Thus the only individual in the first horizontal row deviates from the mean for height by -3, and from that for weight by -4, so that the entry in the ΣP column is $1 \times -4 \times -3$, or 12. In the second row there are two squares represented, $1 \times -3 \times -3$ and 1×0, or 0. In the third row there is one individual which deviates from the mean for height by -3, seven which deviate from it by -2, and two by -1. All these deviate from the mean for weight by -2. The entry in the ΣP column opposite this row is the sum of the product of each of these ten individuals multiplied by their deviations from both means, and may be computed thus:

$$\begin{array}{r}
1 \times -3 \times -2 = 6 \\
7 \times -2 \times -2 = 28 \\
2 \times -1 \times -2 = 4 \\
\hline
38
\end{array}$$

or, more simply,

$$\begin{array}{rcl}
1 \times -3 &=& -3 \\
7 \times -2 &=& -14 \\
2 \times -1 &=& -2 \\
\hline
&& -19 \times -2 = 38.
\end{array}$$

The entry in the ΣP column opposite the next row is

$$\begin{array}{rcl}
1 \times -4 &=& -4 \\
2 \times -3 &=& -6 \\
12 \times -2 &=& -24 \\
9 \times -1 &=& -9 \\
6 \times 0 &=& 0 \\
1 \times +1 &=& +1 \\
\hline
&& -42 \times -1 = 42.
\end{array}$$

The sum of the ΣP column in the example is thus 180.

The formula for r, the coefficient of correlation, is as follows:

$$r = \frac{\frac{\Sigma P}{n} - (c_x \, c_y)}{\sigma_x \, \sigma_y}.$$

By substituting in the present example, the result is:

$$r = \frac{\frac{180}{200} - (+0.69 \times -0.49)}{1.626 \times 1.330} = +0.571.$$

The probable error of r is as follows:

$$E_r = \pm \frac{0.6745\ (1 - r^2)}{\sqrt{n}},$$

which in this example is

$$\pm \frac{0.6745 \times 0.6739}{14.14} = \pm 0.032.$$

The coefficient of correlation between height and weight in the group of 200 men is thus $+0.571 \pm 0.032$.

r may range from $+1.0$ to -1.0, the former being a perfect *positive* correlation (in which the two variables increase or decrease exactly together) and the latter a perfect *negative* correlation (in which an increase in one variable is associated with a proportional decrease in the other). If r is 0, there is no correlation between the variables; and the size of r, which is always a fractional quantity except when correlation is perfect or absolute, may thus be used to measure the degree of correlation. In many cases where r is relatively small, it becomes a matter of importance to determine whether a correlation really exists or not. In a study of a comparatively small number of individuals, this can never be decided with certainty, but the relative probability that a correlation exists may be determined by comparing r with its probable error. If r is at least six times as large as this quantity, the probability of the existence of a correlation is so great as to amount to practical certainty. As the ratio of r to its probable error decreases, the likelihood of the existence of a correlation also decreases, but this decrease is less rapid where the actual value of r is large than where it is small.

TABLE XVII.—WEIGHT, HEIGHT, AND CHEST GIRTH OF 200 MEN (*Data from Department of Physical Education, Connecticut Agricultural College*)

Weight, pounds	Height, inches	Chest, inches	Weight, pounds	Height, inches	Chest, inches	Weight, pounds	Height, inches	Chest, inches	Weight, pounds	Height, inches	Chest, inches
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	142	65	40	130	67	35
156	72	40	118	64	32	143	69	35	135	67	33
163	69	39	130	68	37	158	73	36	119	64	31
128	65	34	146	70	39	127	65	34	139	67	37
126	70	34	137	60	37	195	71	41	130	66	35
142	70	36	159	68	38	144	69	35	144	59	38
156	70	37	154	72	37	130	66	34	119	64	34
132	67	38	131	69	32	133	67	38	172	73	40
156	68	38	124	68	38	133	66	35	136	64	37
144	68	35	134	65	36	161	68	38	137	66	33
157	69	34	150	70	38	141	69	39	137	70	35
162	73	35	131	67	36	152	67	35	136	67	33
147	67	33	129	66	35	114	66	34	136	68	36
124	65	32	156	67	37	141	66	37	133	65	35
114	63	35	134	68	35	130	67	35	136	66	36
152	68	37	111	64	34	130	68	33	143	69	37
127	69	32	171	71	41	175	72	39	185	74	40
146	70	35	135	66	36	140	70	37	135	73	36
130	66	36	140	68	34	127	66	35	148	68	35
115	65	34	141	64	37	124	64	34	142	68	36
135	66	36	145	66	34	116	64	34	147	68	40
131	68	35	122	66	32	125	67	36	149	68	37
174	69	38	123	64	36	145	67	33	139	62	37
130	65	35	121	65	31	155	67	39	112	64	34
151	66	38	140	64	34	128	63	35	170	69	41
176	71	37	140	67	34	131	66	35	148	67	37
140	71	37	137	66	33	147	67	37	123	69	36
133	68	36	165	72	38	142	67	36	144	67	38
127	66	36	135	69	36	148	72	38	141	65	38
142	68	36	162	73	36	150	68	33	142	67	34
135	64	36	128	68	36	131	66	34	142	67	34
126	69	36	130	68	33	135	68	35	122	66	33
148	70	37	156	72	38	139	63	34	121	61	32
139	68	36	144	68	38	125	64	32	148	71	38
123	66	36	132	68	35	173	74	37	157	72	38
150	71	39	173	70	39	154	69	39	107	62	33
160	71	39	152	70	33	134	65	32	148	67	38
140	67	37	136	70	35	151	69	37	176	69	39
134	68	36	128	69	34	158	66	37	135	70	37
153	69	40	134	71	33	135	66	38	119	66	35
135	68	33	120	65	34	135	67	35	95	62	30
141	70	33	148	69	34	127	67	33	174	66	39
127	63	33	162	67	35	165	68	39	133	67	35
144	72	33	145	65	38	153	69	38	150	69	37
130	66	32	166	73	41	169	70	38	141	69	36
123	65	32	142	68	38	165	68	39	138	69	36
141	65	35	122	67	35	140	67	34	122	64	32
134	69	32	126	64	36	150	67	35	166	69	39
160	67	38	109	68	34	153	68	37	160	71	36
133	66	32	149	68	35	141	69	35	171	69	40

QUESTIONS FOR THOUGHT AND DISCUSSION

99. Construct two curves in which the number of individuals and the mean are the same, but which differ considerably in variability.

100. In biometrical analysis why is it justifiable to use a single quantity (the value of the class center V) to describe all the members of a class which may include individuals differing considerably from one another?

101. Two marksmen each shoot three times at a target. The bullets of No. 1 are one foot, two feet, and three feet from the bull's eye, while those of No. 2 are all 2 feet from the target. Which is the better marksman, and how did you decide ?

102. The two parent types in Table XIV have standard deviations of .8 and 1.9 centimeters respectively, and coefficients of variability of 12.3 and 11.1 per cent. Why should the coefficients of variability be so similar when the standard deviations are so unlike?

103. What property of the coefficient of variability makes it superior to the standard deviation as a measure of variability in comparing groups for variability in the same trait?

104. The F_1 generation from pure parent types differing in a size character is usually no more variable than the parents. Explain.

105. If two pure types, differing in a size character, are crossed, is it possible for individuals in the F_2 to be more extreme than either grandparent? Explain.

106. Why is it, when selection has ceased to be effective in producing changes in a given stock, that if this stock is crossed with another similar one, selection among the subsequent offspring is often able to produce a marked change?

107. As a result of crosses involving a size character, it is often found that F_3 families raised from selfed F_2 plants differ markedly in their coefficients of variation. Some are almost as low as the original parents, some a little higher, and some as high as the F_2 itself. None exceed the F_2 in variability, however. Explain these facts.

108. It frequently happens that one character of a plant, such as number of seeds, is much more variable than another character, such as weight of seeds. What explanations for this difference can you suggest?

109. Certain groups of individuals, when their frequency distribution is plotted, show a bimodal or multimodal curve. What different explanations can you make for this fact?

110. Mention three physiological and three psychic characters which appear to be inherited quantitatively.

111. In what way does the multiple-factor hypothesis strengthen the mendelian explanation of inheritance?

PROBLEMS

220. Classify for chest girth the 200 men for whom the data are given in Table XVII, grouping them into classes which differ by 1 inch. Construct a frequency polygon for this group of men as to chest girth.

221. Determine, by use of the short method, the mean, standard deviation and coefficient of variability for chest girth of the 200 men classified in the preceding problem, determining the probable errors in each case.

222. Using the data given in Table XVII, determine the coefficient of correlation between weight and chest girth in these 200 men and its probable error. How many times is r larger than its probable error? On the basis of these figures, do you think that a correlation exists between weight and chest girth in men? On the basis of these figures and those derived in Table XVI, do you think that weight in men is more closely related to height or to chest girth?

223. Assume that the brown color of chaff in oats is due to two duplicate factor-pairs, *AA* and *BB*, white being *aa bb* (Nilsson-Ehle). In the F_2 from a cross between homozygous brown and white, what proportion of the plants, when selfed, will breed true to brown? What proportion will give fifteen brown to one white? What proportion will give three brown to one white? What proportion will breed true to white?

224. Assume that the red kernel color of a certain race of wheat is due to the presence of three independent factors, *A*, *B*, and *C*. Any one of the factors singly will cause the red color. White is *aa bb cc* (Nilsson-Ehle). What are the genotypes of the parents in each of the following crosses: Red × red giving three red to one white; red × red giving fifteen red to one white; red × red giving sixty-three red to one white; red × red giving seven red to one white; red × white giving one red to one white; red × white giving three red to one white; red × white giving seven red to one white; red × white giving all red.

Note.—Assume that the difference in skin color between negro and white is due to two independent factor-pairs, *AA* and *BB*, which do not show dominance over their recessive allelomorphs and which are equal and cumulative in their effect, like the factors for red kernel color in wheat. The negro is thus *AA BB* and the white *aa bb*. Call the grades of color which depend on four, three, two, and one factors, *black, dark, medium, and light,* respectively.

225. What will be the skin color of the offspring from a mating of white with black? from a mating of two individuals genotypically like these F_1 offspring?

226. What are the genotypes of the parents in the two following matings of negroes: Medium × light, giving one-eighth dark, three-eighths medium, three-eighths light, one-eighth white; medium × light, giving one-half medium and one-half light.

227. What will be the offspring of a cross between two negroes with the pigmentation called "light" and "dark" respectively.

228. Can two negroes have white-skinned offspring? Can two white-skinned people have dark-skinned offspring? Explain.

229. Assume that the difference between a race of oats yielding about 4 grams per plant and one yielding 10 is due to three equal and cumulative multiple factor-pairs AA BB CC. Cross one type with the other. What will be the phenotypes of the F_1? of the F_2?

230. Assume that in squashes the difference in fruit weight between a 3-pound type and a 6-pound type is due to three factor-pairs, AA, BB, and CC, each factor contributing ½ pound to fruit weight. Cross a 3-pound plant (aa bb cc) with a 6-pound one. What will be the phenotypes of the F_1? of the F_2?

231. In the following squash crosses, what will be the range in fruit weight of the offspring, on the previous assumption?

$Aa\ Bb\ CC \times aa\ Bb\ Cc$	$Aa\ Bb\ Cc \times Aa\ Bb\ Cc$
$AA\ bb\ Cc \times Aa\ BB\ cc$	$aa\ BB\ cc \times AA\ BB\ cc$

232. A breeder has three squash plants each of which bears 4-pound fruits. Plant 1 when selfed breeds true to 4-pound fruits. So does plant 2. In plant 3 the offspring range from 3 to 5 pounds. Plant 1 crossed with plant 2 gives offspring all of 4 pounds, but *their* offspring when inbred range from 3 to 5 pounds, and selection cannot increase this above 5 pounds. Plant 1 crossed with plant 3 gives offspring which range from 3½ to 4½ pounds, and selection among *their* offspring can raise the fruit weight to 6 pounds. Plant 2 crossed with plant 3 gives offspring which also range from 3½ to 4½ pounds, but selection among their offspring is able to raise fruit weight only to 5 pounds. Give genotypes for these three parent plants which will explain these results.

233. Assume in the following five problems that the difference between a corn plant 10 decimeters high and one 26 decimeters high is due (in so far as it is caused by inheritance) to four pairs of equal and cumulative multiple factors, the 26-decimeter plant being AA BB CC DD and the 10-decimeter one aa bb cc dd. What will be the size and genotype of an F_1 from a cross between these two pure types? Make a frequency

polygon of the F_2 from such a cross. Give the limits of variation in height which the offspring of the following crosses will show:

$Aa\ BB\ cc\ dd \times Aa\ bb\ Cc\ dd$ $\qquad AA\ BB\ Cc\ DD \times aa\ BB\ cc\ Dd$

$aa\ BB\ cc\ dd \times Aa\ Bb\ Cc\ dd$ $\qquad Aa\ Bb\ Cc\ Dd \times Aa\ bb\ Cc\ Dd$

234. Two 14-decimeter corn plants, when crossed, give nothing but 14-decimeter offspring. Two other 14-decimeter plants give one 18-decimeter, four 16-decimeter, six 14-decimeter, four 12-decimeter, and one 10-decimeter plants. Two other 14-decimeter plants when crossed give one 16-decimeter, two 14-decimeter, and one 12-decimeter plants. What genotypes for each of these 14-decimeter parent plants would explain these results? By selection in any of these families would it be possible to get a plant taller than 18 decimeters?

235. A breeder has a number of plants which are 14 decimeters high. He crosses some of these together, selfs their offspring, and selects among their offspring for increased tallness, for several generations. His results are as follows:

Two throw all 14-decimeter offspring, and selection fails to raise their height.

Two others throw offspring varying from 10 to 18 decimeters, and selection among these fails to raise the height above 18 decimeters.

Two others throw offspring varying from 12 to 16 decimeters, and selection is able to raise the limit to 22 decimeters.

Two others throw offspring varying from 10 to 18 decimeters, and selection is able to raise the limit to 22 decimeters.

Two others throw offspring varying from 10 to 18 decimeters, and selection is able to raise the limit to 26 decimeters.

Explain, by giving parents' genotypes for height, why these results obtain.

236. A breeder has a 26-decimeter starchy and a 10-decimeter sweet corn. Starchiness is dominant over sweetness and is due to a single factor. He wants a 26-decimeter sweet corn. Assume that height is due to four factor-pairs, as before. If he wants this new type of corn in two years, how many plants should he raise in the F_2 of the cross between tall starchy and short sweet to be reasonably sure of getting it? If he has more time, what would you advise him to do in order not to have to raise such a big crop in the F_2 and subsequent generations?

237. Suppose that the difference between a 26-decimeter and a 10-decimeter corn plant is caused by four pairs of multiple factors (as in the previous examples) and that the difference between a one-stalked and a 9-stalked corn is also due to four other pairs of cumulative multiple factors. A breeder has a 9-stalked, 10-decimeter race and a one-stalked, 26-decimeter race. He wants for silage corn a pure race 26 decimeters high, with 9 stalks. If he wants it in two years, how many

plants should he raise in the F_2? By spending more time how can he get it more easily?

238. Arrange the following individuals, the genotype of which is given for five factors, according to the coefficient of variability which their selfed offspring will show, placing the highest first:

AA bb Cc Dd EE	*Aa bb Cc dd ee*	*AA BB Cc Dd Ee*
aa Bb cc dd Ee	*aa bb cc dd Ee*	*aa bb cc dd ee*
Aa Bb Cc Dd ee	*Aa Bb Cc Dd Ee*	*AA Bb Cc dd ee*
Aa Bb cc DD Ee	*Aa bb cc DD EE*	*AA BB cc DD EE*
Aa bb cc dd ee		

239. If the difference in ear length between a variety of corn producing ears 18 centimeters long and another ears 30 centimeters long is due to three equal factor-pairs, and plants of these two varieties are crossed, what will be expected proportion of each of the seven length-phenotypes in the F_2? What will be the mean, standard deviation, and coefficient of variability of such an F_2 (disregarding environmental influences)?

240. In the two following crosses and their progeny, involving a size character, in which case do you think that the larger number of multiple factors is involved? About *how many* factors are involved in the second case? Explain fully.

P	4	7	3	..	..	..	..	..	..	4	5	1
F_1	..	..	..	..	2	7	6	1				
F_2	..	..	..	3	15	18	12	4	2			
P_1	3	4	2	..	..	..	..	..	1	5	4	2
F_1	..	..	..	..	4	6	5	2				
F_2	1	1	2	3	5	9	6	4	3	2	1	1

241. Calculate the standard deviation of the F_2 ratios obtained from crosses of individuals differing in one, two, three, and four size factors which do not show dominance. Does the increase in the number of factor differences between the parents increase or decrease the variability of F_2?

REFERENCE ASSIGNMENTS

72. Describe two specific problems in fields other than genetics in the study of which biometric methods have played an important part.

73. What is the median? How is it calculated? What is its use?

74. Explain the method for determining whether the difference between two given biometrical constants is a significant one or not, by comparing this difference with the probable error of the difference.

75. How would you determine whether the deviation of an actual from an expected mendelian ratio is statistically significant or merely accidental.

76. Describe the product-moment method of calculating the coefficient of correlation.

77. What is regression? How is it measured, and what is its relation to correlation?

78. What evidence is there that the various members of a series of multiple factors may have unequal effects?

79. The inheritance of some quantitative traits has been described as *blending*. What is meant by this term? Do you think that quantitative traits are inherited in this way? Explain.

80. Describe two examples from plants and two from animals of quantitative characters which show dominance.

81. Do organisms differ in size because they have larger cells or because they have more cells?

82. Define the following terms:

Variate
Integral variates
Graduated variates
Quartile
Frequency
Random sample
Skewness

CHAPTER XI

TYPES AND CAUSES OF VARIATION

In the second chapter attention was directed to the universal occurrence of *variation* in animals and plants, and it was shown that even among closely related individuals there often appear

Fig. 92.—Extreme variations in human stature. (*From Journal of Heredity.*)

marked differences in structure and activity. The major interest of the geneticist is to discover how these variations behave in inheritance, and the greater portion of this text has consequently been devoted to a study of the manner in which the segregation

and recombination of genetic factors, carried from parent to offspring in the gametes, regulates the hereditary transmission of these traits.

It is evident, however, that a knowledge of the laws by which these differences are distributed in inheritance is only one step toward an understanding of variation as a whole. The question at once arises, for example, as to where and how these hereditary differences originate. Everyday experience indicates that much of the variation observed is not determined entirely by the inheritance which an organism receives, but in considerable measure by the environment under which it lives and develops. It is, therefore, important to be able to recognize the effects which are due to each.

Variations are of many types and due to many causes, and the problem which they present is too complex to be solved by the application of any simple formula or law. In the present chapter, therefore, the chief types of variation will be described and their causes explained, so far as these are known.

Variation.—Variation may be considered as any difference between related organisms. Variations may be as gross and noticeable as those which differentiate the human freaks in the circus from normal men and women (Fig. 92), or they may be as small and insignificant as slight departures from regularity in the arrangement of the teeth. They may be continuous and quantitative (Fig. 93), as are most variations in weight, height, and other similar features, or they may be distinct and apparently qualitative, as the differences among men in eye color. Variation may affect structural features, as in the cases above mentioned; it may be primarily physiological, as with differences in fertility or disease resistance; or it may affect behavior or mentality. Since no single part or function of any plant or animal is exactly like that of any other, it is apparent that variations may affect any part or process, be of any kind or size, and may or may not be heritable. They might thus be classified in a variety of ways, but it will be most useful to analyze them in a manner which will lead to some understanding of the causes that produce them and to a decision as to whether or not all are equally heritable.

It must be admitted at the outset that very little is definitely known about the origin of most of the variations which have been discussed in this book. Such familiar characters as the colors of rodents or fowls or the simple qualitative variation

in corn have arisen by processes which remain mysterious even after the details of inheritance have become well known. It is

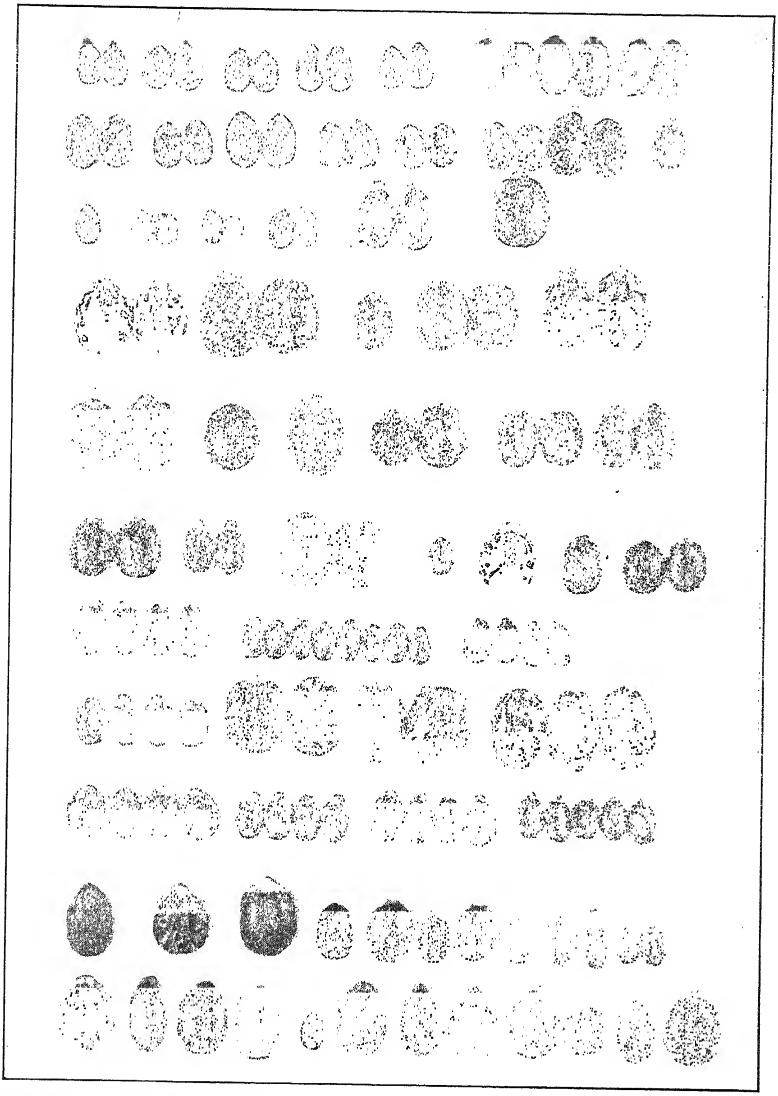


FIG. 93.—Variation in shape, size, color and pattern of castor beans. (*From White, in Journal of Heredity.*)

already possible, however, to be certain that not all variations are alike in origin, since some are obviously correlated with

factors in the *environment*, whereas others have shown no such correlation but seem to have arisen spontaneously from causes *within the organism*. In the discussion which follows, variations have been grouped into these two classes, although this classification must not be regarded as a hard-and-fast one, but merely as representing present limited knowledge. Most characteristics of the organism are in the nature of responses to external stimuli, of one kind or another, and although some variations appear at present not to be responses of this sort, this may be due only to the fact that the stimuli which call them forth have not yet been discovered.

Environmental.—In the first category, then, may be placed those variations caused by influences in the *environment* of the organism. The term environment, while usually referring to the sum of all external influences, may include factors of various sorts operating within the body, such as disease, substances in the blood, or other agencies. Under this heading will be discussed and illustrated variations directly traceable to nutrition, temperature, climate, and so on, and an attempt will be made to determine whether such variations are subject to any laws of inheritance. This will lead to a discussion of the debatable question of the inheritance of acquired characters, with its bearing on the various theories as to the methods of evolution and of plant and animal improvement.

Autogenous.—In the second category may be placed those variations which do not appear to be correlated with environmental agencies and which are probably due to changes or rearrangements originating *within the organism*. Such variations may be called *autogenous*, since in the present state of knowledge they appear to originate spontaneously. Here will be found to fall nearly all of the hereditary traits thus far considered. A discussion of their origin and nature involves reference to (1) new characters arising from the segregation or recombination of latent or previously unexpressed factors; (2) sudden changes or mutations in the hereditary material; (3) changes in the number, nature, or arrangement of the chromosomes which carry the inherited factors, and (4) permanent changes in the vegetative as distinguished from the reproductive tissues, as in the case of bud variations.

Criteria for Distinguishing the Different Types of Variation.—The two categories of variations distinguished in respect to

origin, are thus *environmental* (qualified as above), and *autogenous*. Any given variation cannot be placed in either of these categories by inspection alone, and it is important to know how one may determine to which it belongs, for most of the traits which can be manipulated by mendelian methods probably belong in one of the autogenous classes and seem not to owe their origin to the environment. If an alteration in the environment produces modification of the varying character, it is probable that the variation is to be classed as an environmental one; if it does not, the character is probably autogenous. A florist may thus observe among plants from the same lot of seed several which are very pale green or white, and may note at the same time that these are growing in a shaded part of the greenhouse. On exposing them to full sunlight he observes that they become green like the others, and concludes correctly that white is in this case an environmental variation induced by lack of sunlight. He may repeat this experiment, however, with another white seedling and find that in either darkness or light it remains white. Many investigators have observed albinic seedlings of this sort and have found that some of these variations are due to internal inherited changes which are independent of the conditions of light.

Some parts of the organism are apparently influenced greatly by the environment, whereas others are not. Thus European cattle introduced into South Africa undergo changes in size, shape, and certain other general characteristics, while their color, markings, and horn characters remain unchanged. Likewise plants exposed artificially to an increased or decreased length of day undergo marked changes in time of flowering and character of leaves, while other traits such as the color of the flowers are not altered. It is obvious that variations of the one sort are environmental, while those of the other sort are internal or autogenous in origin.

This classification, however, is not so simple, nor so definite as would appear from such cases, for no variation is conditioned by internal or by external factors exclusively. In this connection the case of the primrose whose flowers are always red if grown under one temperature, and white if grown under another, should be recalled (page 26). Among the varieties of rabbits is one known as Himalayan which is white with black "points,"—nose, ears, tail, and toes. If the white fur is plucked or cut from

such rabbits and they are then exposed to cold while the new fur is growing, this new fur is *black* (Fig. 94). Black in this case might be called an environmental variation. It is also an expression of internal factors, however, since if the genotype of the albino includes a gene for agouti, the new hairs are banded as in the agouti pattern, but otherwise are plain. These are a few instances of the general rule that each internal variation or factor is but the expression of an ability to *respond in a specific way to a particular set of external conditions.* Therefore, in classifying variations as external and internal in origin it should be realized that external and internal conditions are interdependent; that

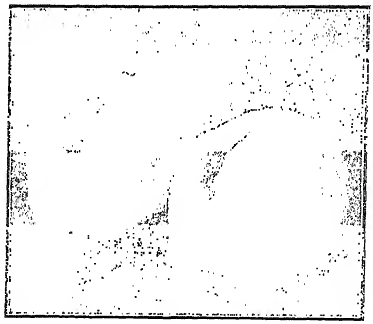


Fig. 94.—The effect of temperature on hair color in rabbits. The white hair on a small area of the backs of these Himalayan rabbits was pulled out and the animals then placed in a cold room. The hair which later grew in was *black.* Hair regenerated in a warm temperature is usually white. (*From Laura Kaufman, in Biologia Generalis.*)

internal variations are due chiefly to a change in the character of the response; and that environmental or external variations are due chiefly to some change in the agencies which call forth the response.

Environmental Variations.—It is not difficult to see that many of the differences between related plants and animals are directly or indirectly due to differences in their external or internal environments. The chief external factors which produce these differences are food, climate (temperature, altitude, humidity), light, and other chemical or physical agents; whereas in the case of animals such internal conditions as disease, secretions of ductless glands, and use and disuse of parts are also to be reckoned as potent causes of variation.

Food.—Among animals differences in the *amount* of food may be responsible for great differences in size. The two steers shown

in Fig. 13, page 28, were born on the same day. One was fed liberally; the other was given only enough food to keep it alive. At two years of age one weighed 1,610 pounds while the other weighed 361 pounds, or about a fourth as much.

Other striking variations are caused by differences in the *kinds* of food supplied. Figure 95 illustrates the profound effect which may be caused by a difference in the quality of the protein supplied to a growing animal.

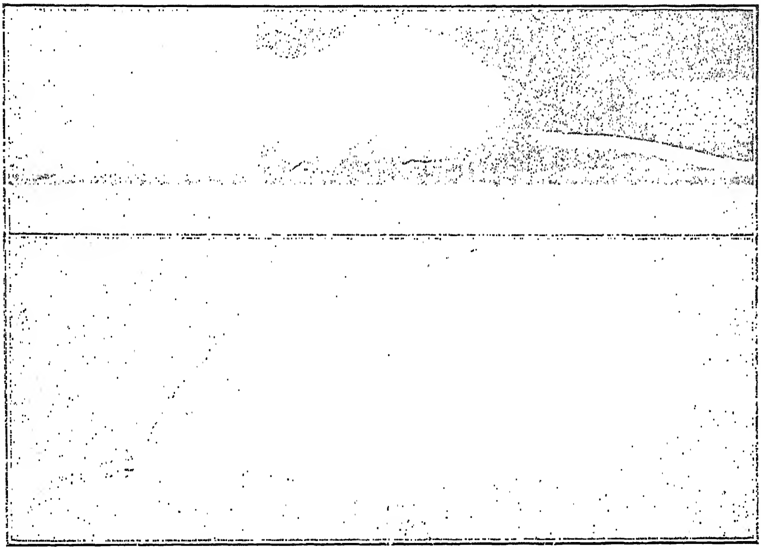


Fig. 95.—Effect of separate components of the diet on growth. The upper photograph shows a rat which had been fed for seven months a diet containing zein (one of the proteins from corn) with a small amount of tryptophane. On this diet the rat could live but not grow. The lower photograph shows the same rat a few months later after casein from milk had replaced the zein and tryptophane. (*Courtesy of Osborne and Mendel.*)

It is now well known that if chickens of a variety which normally has yellow shanks, beaks, and skin are fed on colorless food (white corn, for example), these parts become white, while if yellow corn or green food are added to the diet, they regain the normal color. This induced variation is of especial interest, since it duplicates a genetic variation which occurs in certain breeds whose shanks and skin are white regardless of what their ration may be.

Many other variations are traceable *indirectly* to amount or kinds of food. In some animals which have been fed a meat

diet the intestine is much shorter than it is in others of the same kind which have been fed a vegetable or mixed diet. The strong jaws and muscles, and the peculiar shape of the face of peoples like the Eskimos who live on food which requires hard chewing, have similarly been thought to be due in part directly to the peculiarities of their diet.

Among plants, nutrition and location must be considered together in their effect on variation, for the plant is stationary and dependent on the nutrient materials in the area covered by

FIG. 96.—Variation due to crowding. Well-spaced corn plants at the left; crowded ones of the same variety at the right. (*From Blakeslee, in Journal of Heredity.*)

its own root system. The stunting effects of crowding on plants are well known and are due chiefly to deficiency of nutrients (Fig. 96). Isolated or properly spaced plants in good soil have an adequate supply not only of mineral salts but of sunlight and water and may attain to several times the size of crowded or starved ones.

Variations due to insufficient nutrients in plants, as in animals, are not confined to differences in size alone, for absence of any necessary element is accompanied by characteristic changes in the form, color, and productivity of the plant. A lack of iron in the soil is reflected in a defective development of chlorophyll, and the appearance of yellow or etiolated plant parts instead of

normal green ones. Inability to perform efficiently the function of photosynthesis is a variation which usually appears in plants receiving insufficient potassium. The object of the application of fertilizer is an attempt to supply all the essential elements and thus to induce the most favorable variations in growth and yield.

Water.—Many of the most extreme variations in plants are produced by differences in water supply. Some forms like the water buttercup are "amphibious," and able to grow either on land or in water. When growing on land, this plant has typical buttercup leaves but when growing in water, its submerged leaves are finely divided and quite different from the normal type. The same kind of variation is found in some other plants (Fig. 97).

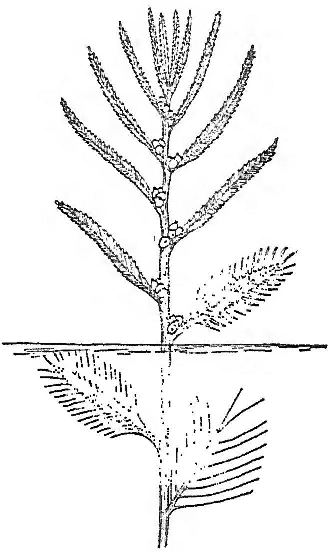


Fig. 97.—An amphibious plant, the mermaid weed (*Proserpinaca palustris*) showing the variation in leaf form between the submersed leaves (finely divided) and the aerial leaves (undivided).

The variations called forth by differences in the amount of water in air or soil are almost as striking. Plants in dry soil tend to have compact limited growth, a more extensive root system, and leaves which are smaller, thicker, or fleshier than plants which are better supplied with water. The rank growth of many tropical plants is due chiefly to their moist, humid environment.

The amount of moisture in the food or in the atmosphere has an intimate relation to a number of variations in animals. In one strain of *Drosophila*, the abdomens of most of the flies are abnormally segmented and deformed when grown on moist food (Fig. 45, page 116). When flies of the same strain are raised on dry food, most of them have normal abdomens. A moist atmosphere has been found to increase the amount of dark pigment developed in some varieties of pigeons, and the lighter pigmentation of some desert rodents has been thought to be an environmental variation influenced by the arid atmosphere.

Temperature.—The characters developed by a given plant or animal depend in some degree on the temperatures to which

they are exposed during growth. A castor bean plant reared in the tropics under uniformly high temperature assumes a tree-like form which differs markedly from the herbaceous habit of the same species reared under the variable and lower average temperatures of the temperate zone. Animals living in colder regions develop thicker coats of fur than those of the same kind in warmer climates. Several cases have already been cited of the changed response of the same plant or animal to different temperatures, as the primrose, which produces red flowers at low temperatures and white flowers at higher ones, and the development of black fur by albino rabbits exposed to the cold.

Light.—One very important element of the environment of plants and animals is light, and it has been found that both its amount and its quality are concerned in the production of specific variations. In the absence of light, green plants can make very little growth because of their inability to carry on the essential process of photosynthesis. Two plants from the same lot of seed, one grown in the dark, the other in the light, come to differ very strikingly in almost all of their characters. The plant grown in the dark is paler, taller, and more spindling than the one reared in the light. Such a plant is not able to mature, and does not flower or set seed (Fig. 98). Alteration in the relative amount of light, especially in the length of daily exposure to light, also brings about important differences in plants, particularily with reference to the relation betweeen their vegetative and reproductive activities. Garner and Allard find that a relatively short daily period of illumination retards the growth of some species and that these will grow vigorously and reach reproductive maturity only if the days are relatively long (Fig. 99, lower). There are other species, however, in which the effect of short days is to hasten flowering and fruiting, activities which may be indefinitely deferred if the plant is exposed to long daily illumination (Fig. 99, upper). Light may also have a direct effect on certain characters, as in the variety of corn previously described in which certain parts of the plant turn red when exposed to sunlight, while unexposed parts remain green. Such examples illustrate well that the characters of plants depend on a complex chain of reactions, some of which can take place only in the presence of a given amount or kind of light.

Some animal variations are likewise due to variations in the light to which they are exposed. A deficiency of the long violet

rays may, under certain conditions, produce marked lesions in the bones of young animals. The condition among young

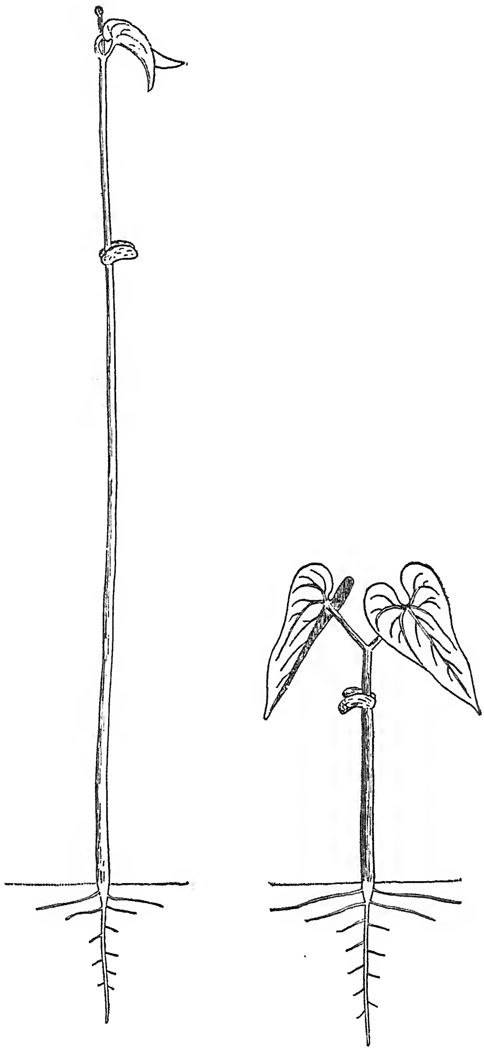


Fig. 98.—Variations in bean seedlings due to differences in light. The spindling, etiolated plant at the left was grown in the dark, and the normal one at the right was grown under normal illumination.

chickens which is known to poultrymen as leg-weakness frequently arises in birds reared indoors or out of direct sunlight.

FIG. 99.—Variations caused by differences in the daily period of illumination. The plants at the left have been exposed during growth to relatively short daily illumination; those at the right to a relatively long one. Above, plants of *Cosmos*, a "short day" plant, in which flowering is hastened by shortened days. Below, red clover, a "long day" plant, in which a shortened day greatly retards flowering. (*From Garner and Allard.*)

Direct summer sun or exposure to ultra-violet light may both prevent and cure this condition.

Altitude.—Some of the most striking differences among plants are those which occur between members of the same species grown at different altitudes (Fig. 100). Mountain plants are generally smaller and more compact than plants living in lowlands. That such differences may be almost wholly environmental is shown by several experiments in which the same plant has been subdivided, half being grown at a low and half at a high or mountain level. The part of the plant transplanted to the mountain assumed a dwarf compact habit, while the part

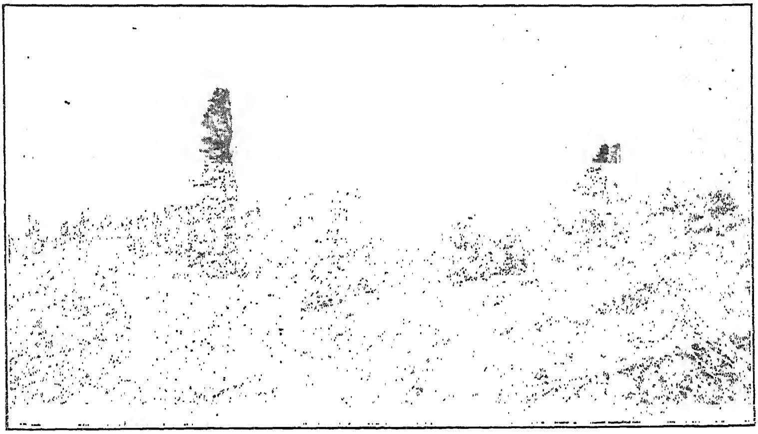


Fig. 100.—Variations due to the environment. Spruce trees growing on an exposed and wind-swept mountain side. Many are reduced to stunted shrubs and the others bear branches only on the side of the trunk away from the prevailing wind.

remaining in the valley exhibited greater and more spreading growth.

The effects of high altitude are no less important in animals, although here the variations induced are chiefly physiological and due to pressure and other factors dependent on altitude. In both plants and animals it is difficult to separate the effects of such subsidiary factors as relative humidity, water supply, and temperature, but it remains a fact that organisms living at different levels come to differ significantly.

Domestication.—The kinds of variations induced by the environment are well illustrated by the evident differences existing between wild and domesticated animals and plants of the same

species. Many of these have doubtless been intensified by selective breeding, although there can be little question that some are due directly to the conditions of domestication, such as better and more regular food, and protection from drought, famine, and natural enemies, among animals; regular tillage, fertilization of the soil, and reduction of competition with other plants, among cultivated plants. Many variations in anatomical

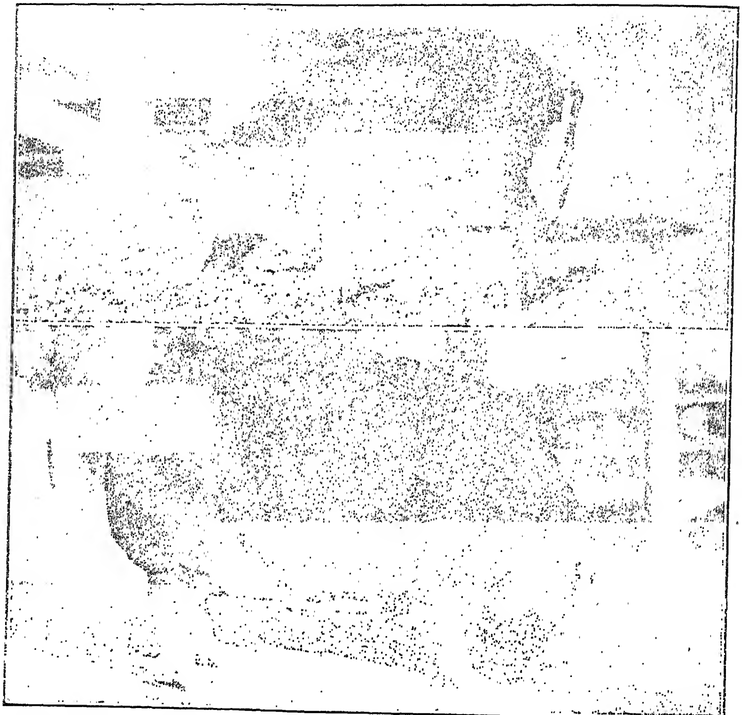


FIG. 101.—The effect of domestication. Above, a wild "razor-back" hog; below, a purebred domesticated hog. (*Courtesy of the Bureau of Animal Industry, U. S. Department of Agriculture.*)

characters, too, have been ascribed directly to domestication. The changes in the teeth, shape of jaw, and general facial and cephalic contours which distinguish modern man from his more primitive ancestors are thought by some to have resulted from his changed diet, mode of living, and other conditions which accompany domestication or civilization. In all such cases the action of natural or artificial selection on autogenous variations may also play a part, but since it has been found that single

factors of the environment may induce variation, it is certain that the combined action of many factors which operate under domestication may alter the characters of the individual animal or plant (Fig. 101).

Internal Conditions.—In the higher animals many forces operating within the organism act like factors in the external

FIG. 102.—A litter of dead hairless pigs farrowed by a sow which had an insufficient supply of iodine in her diet. After iodine was added to her diet, later, her litters were normal. (*From Hart.*)

environment in inducing variation. The ductless glands or endocrines, for example, secrete chemical substances known as hormones into the blood stream. These reach all parts of the body and regulate or control the development of many characteristics. Variations in these glands or their secretions produce many secondary variations in the animal body. In mammals

and birds secondary sexual characters such as size, voice, instincts, plumage form and color, and comb form are dependent on the hormones produced by the ovary and testis, and when these glands are removed or destroyed typical variations in the sexual characters are induced (page 199). A peculiar variation in pigs has recently been traced to a hormone deficiency. Occasionally young pigs at birth are weak, sickly, and completely devoid of hair. The factor causing this variation is apparently a deficiency in the thyroid secretion of the mother, and it may be prevented by feeding iodine, the active principle of the thyroid secretion, to sows during pregnancy (Fig. 102). In this case, as in a number of human diseases such as myxoedema and cretinism, an environmental factor such as iodine or thyroid extract in the diet may take the place of an internal secretion which has become deficient either from environmental or from inherent causes. A very important physiological variation, immunity for specific diseases, may also be acquired by a change in the internal environment brought about in this case by the injection of antitoxins or immune sera.

The obvious conclusion to be drawn from all such examples is that many of the variations exhibited by animals and plants have a direct relation to the conditions under which they live. It becomes, therefore, a question of great theoretical and practical importance to determine whether these variations of which the causative factors are known are or may become *hereditary*.

The Inheritance of Acquired Characters.—At first glance it might seem that the inheritance of such environmental variations would offer the most obvious explanation of the origin of new heritable traits. It has frequently been assumed that small or dwarf races of animals and plants are descended from ancestors which for many generations were subjected to an inadequate food supply, adverse climate, and other conditions which are known to limit growth in size. Specific variations such as hornlessness or taillessness might also be thought to have arisen from the practice of dehorning or of docking the tail continued over many generations. During the last century such hypotheses have been subjected to many tests by experiment, and although the verdict of many of these experiments is inconclusive, it is possible to derive some definite answers from the data.

The general problem is whether variations induced in animals and plants by the action of the environment may become

inherited or not. This question is of importance both for the student of genetics and for the animal and plant breeder who must know whether the characters with which he deals arise in this way, whether they may be transmitted from parent to offspring, and whether they may be induced at will; and for the student of evolution, who must know whether the heritable characters of existing animals and plants owe their being to variations originally induced in their ancestors by the action of environmental factors.

Historical.—Lamarck, a French biologist (1744–1829), was the first modern thinker to recognize the problem clearly and to

FIG. 103.—Jean Baptiste Lamarck (1744–1829). (*From A. F. Shull, after Locy.*)

offer an explanation of the origin of variations and of the method of evolution (Fig. 103). He supposed that variations were induced in the individual by such external and internal agencies as the direct action of the environment or the use and disuse of a part, or that they arose in response to an urgent need on the part of the organism. The characters so called into being he regarded as truly heritable, and the environment which had directly or indirectly caused variations to appear was in his theory the directing agent in evolution. To Lamarck *all* variations were acquired and *all* variations were heritable. Darwin, who established the

theory of organic evolution, made little inquiry into the causes of variation, although like Lamarck he thought that some, at least, originated through the direct action of the environment. He regarded most of the hereditary changes in the organism as spontaneous variations of unknown nature, and these provided the differences in adaptability from which the environment selected the best or fittest to survive. Darwin foreshadowed the modern view of the question by recognizing that not all variations were

FIG. 104.—August Weismann (1834–1914). (*Courtesy of Genetics.*)

due to a single set of causes and that not all were equally heritable. Weismann, following Darwin, established this distinction and showed that many variations caused by the environment or artificially induced, such as mutilations or injuries, were not inherited, while variations of another kind were inherited. The latter, the cause of which he did not know, he called congenital or germinal, as distinguished from acquired or environmental variations.

In support of his contention that characters acquired by the organism were not inherited, Weismann developed the *germ-plasm* theory, which considers the reproductive tissue (the germ cells) as separate and distinct from the other tissues of the body (the *somatoplasm*). The environment, Weismann believed,

was able to cause many variations in the somatoplasm, but such changes could not be transferred to the germplasm (which was the sole seat of hereditary characters) and, therefore, could not become inherited. Some experimental evidence for the non-inheritance of such acquired characters as mutilations and some evidence of the structural and physiological independence of body and germ cells in higher animals was obtained by Weismann and has been added to and corroborated by later investigators.

A classic experiment to determine whether the characters of the body influence the inherited constitution of the germ cells was

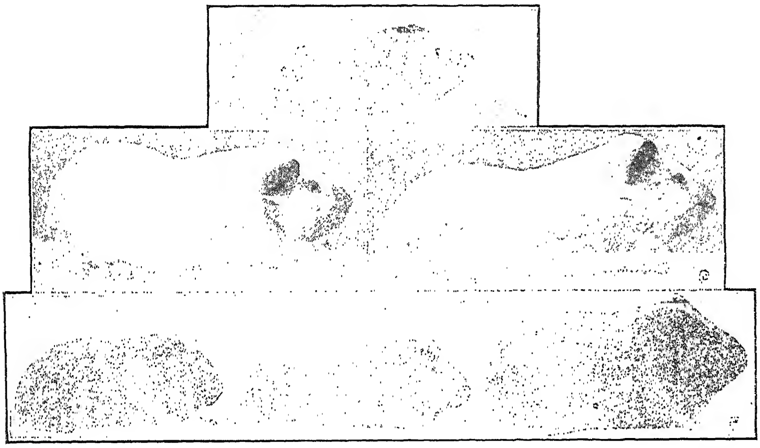


FIG. 105.—Results of ovarian transplantation in guinea pigs. Ovaries from a black guinea pig (*A*) were transplanted into an albino female (*B*) which, when mated with an albino male (*C*) produced black young (*D*, *E* and *F*). (*From Castle*).

performed by Castle and Phillips. They transplanted the ovaries from a black into an albino guinea pig which had been deprived of its own ovaries. After recovery from the operation this albino female was mated with an albino male. This mating produced *only black offspring* some of which were born a year after the operation. Matings of two normal albino guinea pigs always produce offspring which are all albinos, since albinism is recessive and thus breeds true (Fig. 105). Th germ cells formed by the "black" ovary apparently retained their own inherited nature with regard to color even after a year's residence in a

"white" body. So far as this trait is concerned, the distinction between body and germ cells is evidently sound.

Although the conception of a distinct germplasm is useful and aids in explaining many facts and in planning experiments with higher animals, it is undoubtedly of limited application. It does not apply at all in the lower animals, where no practical distinction between soma and germ can be made, nor in plants, where many or all parts of the plant body may give rise to germ cells or to new individuals without the intervention of a sexual process. Even in the higher animals it is possible that the gametes may arise from tissue which is not fundamentally different from that which produces other parts of the body, and that the gonads are not completely insulated from those forces which effect changes in the body tissues.

Statement of the Problem.—Although the existence of the mechanism by which acquired characters might be transmitted to the germ cells has not been demonstrated, there is no necessary or inherent impossibility of its existence, and the question to be settled by the experimental evidence is simply whether such characters do or do not become inherited. Before presenting the evidence which has been gathered, the problems involved must be carefully stated.

1. *Transfer of Effects from Body to Germ Cells.*—The first question to be examined is the apparently simple one as to whether such variations as have been cited above, which are produced by the action of environmental factors, use, or habit on the tissues of adult or developing organisms, are ever inherited. These variations represent the responses of the animal or plant to external stimuli, and this responsiveness or sensitiveness is known to be a general property of all living substance. The point at issue is whether the particular response made by an ancestor (as, for example, the greater growth reaction of plants to good soil or of animals to food, heat, or light) has any determining effect on the responses to be made by its descendants. Does the fact that the parent has responded in a certain way leading to a visible variation predetermine the response of the offspring, or make it any easier for the offspring to develop this same character in the absence of the same stimulus? If it does, it will mean that the characters acquired by the adult organism may be transferred and impressed on the germ cells and affect all future generations. Darwin in his theory of pangenesis proposed

a mechanism by which such a transfer might take place. He imagined that each part of the body might send representatives or *pangenes* to the germ cells through the blood stream, and that if a specific change in any part took place, this might be reflected in its representatives and thence in the germ cells and the succeeding generations to which they gave rise. Darwin himself did not seriously entertain this speculation, and it was easily refuted by simple blood-transfusion experiments. It is presented here merely to illustrate one kind of theory required by the supposition that bodily alterations may become incorporated in the germ cells.

2. *Parallel Induction.*—Do environmental or other stimuli affect the germ cells *at the same time with*, rather than *by way of*, the body? May such agencies as heat or poisons, for example produce changes in the germ cells which may then be transmitted to further offspring? This possibility is usually referred to as the *parallel induction* of changes in the parent and its germ cells.

3. *Production of Mutations.*—Is there any evidence that conditions external to the germ cell may alter its hereditary constitution by inducing the formation of new genetic factors or by changing the existing ones? In other words, can the environment induce mutations?

Questions of all three sorts are usually included in the question "Are acquired characters inherited?" but it can be seen that in a narrow sense the only "acquired characters" are those in the first question. In a broad sense, however, answers to all three are quite germane to a discussion of the rôle of the environment in causing heritable variations.

The Evidence.—Some of the evidence bearing on these questions will now be summarized. The evidence is most conveniently grouped under several external or internal agencies which might conceivably cause inherited variations. Answers to the three questions will then be derived from the evidence.

Passive Transmission.—It is well known that certain dyes fed or injected into a female bird may find their way into the eggs and reappear in her progeny. An acquired effect has in this case been certainly transmitted from one generation to the next. It is equally certain that such a process does not represent inheritance in the sense in which we have used this term, since the egg has simply served as the vehicle of transmission of a foreign substance from one generation to the next. The process

simulates inheritance and might be called pseudo-inheritance or passive transmission.

A similar method of transmission is followed by several diseases of which the best known is syphilis. This disease is caused by a protozoön parasite and may be acquired by the mother through external channels of infection. The children of such a mother frequently develop the disease when reared apart from the mother and guarded against infection. They may, moreover, transmit syphilis to their children. In this case it is known that the protozoön parasite itself passes into the egg cells of the syphilitic mother, and, like the dye, is passively transmitted to the progeny. In fowls, the bacillus causing white diarrhoea in young chicks may be acquired by the hen, pass into her eggs, and cause the disease in her progeny. The diseases known as pebrine in silk moths and Texas fever in cattle are similarly transmitted through the egg.

The heritability of other acquired diseases, as such, can rarely be established, since it is difficult to eliminate the possibility of infection of the embryo or new-born young by the mother. Early infection probably accounts for the frequent occurrence of tuberculosis in the offspring of tuberculous mothers, although in this as in similar cases it is possible that a predisposition or susceptibility toward a disease may really be inherited. There is also evidence that antitoxins and immune bodies, acquired by the mother, which increase her resistance to a specific disease or toxin may be transmitted to her progeny. The male has not this power, nor has such acquired immunity been shown to have been transmitted to more than one generation.

In these cases it is evident that there has been no change in the hereditary constitution. An acquirement has been transmitted *with* the hereditary material, but has not itself become a part of it. This clearly shows that reappearance of a parental condition in the progeny cannot always be taken as evidence that it is truly inherited.

Poisons and Other Chemical and Physical Agencies.—Closely allied to the inheritance of acquired diseases is the possible inheritance of variations induced by the administration of poisons, stimulants, or similar chemical agencies. A large number of experiments have shown that striking changes may be wrought in animals by changing the normal chemical composition of the surroundings or the diet. In marine animals (such as fish and

echinoderms) monstrous and bizarre forms may be produced by slight changes in the proportion of various salts present in the water. One-eyed, partially double, and both dwarf and giant forms have been produced in this way, but there is no evidence that such variations are heritable. In the higher animals alcohol has frequently been employed. Stockard obtained many abnormal embryos and young showing numerous types of defects following the administration of alcohol to guinea pigs. He interpreted these variations as due to direct injury to the germ cells by alcohol. They reappeared in the unalcoholized offspring of defective animals, showing that such injuries may persist

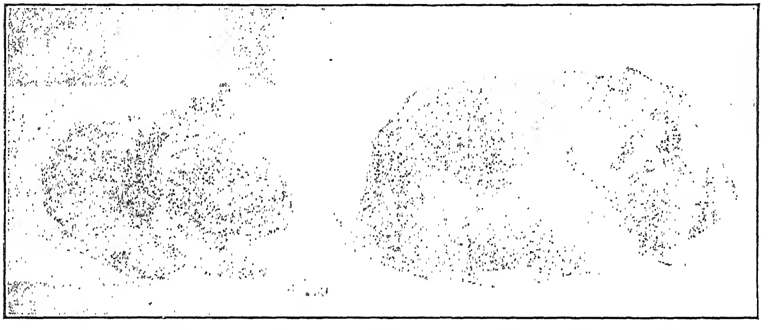


Fig. 106.—Guinea pigs from alcoholized ancestors. On the left a small degenerate guinea pig, six of whose eight great-grandparents had been treated with alcohol. On the right a normal guinea pig born the same day. (*From Stockard.*)

for more than one generation (Fig. 106). A number of other experiments, however, have shown that alcohol may act selectively to kill the weaker germ cells and allow the stronger to survive. Thus MacDowell, working with rats, found that while alcohol administered to the parents reduced the fertility, the learning speed, and the capacity of untreated descendants, these same rats grew more rapidly than the descendants of untreated parents. Pearl obtained fewer but more vigorous progeny from alcoholized than from unalcoholized fowls. A poison such as alcohol may, it seems, kill the weaker germ cells and embryos, and may produce injuries of a general nature which may persist in the descendants. Experiments with more rapidly reproducing animals of which more generations may be observed, make it appear probable that these injurious effects do not

persist through an indefinite number of generations as an inherited variation should, but that the effect of injury to ancestral germ cells gradually wears off.

Experiments on the induction of specific factor changes by the use of poisons have in general provided only negative evidence. Thus fruit flies have been reared on media containing arsenic, quinine, morphine, alcohol, and other poisons, and although several of these reagents caused marked variations in the treated flies, these were not inherited, nor did any new inherited factors arise as the result of such treatments.

Mutilations.—The clearest cases of the non-inheritance of acquired characters have been supplied by a study of the descendants of mutilated or injured individuals. Experiments, either deliberate, unplanned, or natural have been performed on many kinds of animals. The dehorning of cattle, the docking of tails of horses and sheep, circumcision, and artificial deformation of feet and heads have been practiced by different peoples for many generations; yet no effect of the injury to the parents is to be traced in their descendants. Weismann cut off the tails of mice for nineteen generations but did not observe any shortening or change in the tails of mice of the later generations. The evidence is such that it would seem to make possible a definite statement that the effects of mutilations are not inherited, and yet even here caution is necessary in drawing sweeping conclusions, for it is possible, though not proved, that some sorts of mutilations may set up reactions within the animal body, which may affect the germ cells. Thus, injuries to one eye may frequently induce the formation of antibodies in the blood under the influence of which the remaining eye may be affected, and several investigators believe it possible that these antibodies may affect the factors for eye characters in the germ cells.

Amounts of Food.—Variations in nutrients supplied to plants chiefly affect size and productiveness. The plant will not tolerate extreme deviations in this respect, such as the absence of any essential element, and the chief variations which can be studied are, therefore, those in amount of nutrients supplied. If plants are starved, they are small and produce small seeds. If such small seeds are planted, the progeny are frequently small, even when grown in fertile soil. This, however, does not represent a permanent inherited change, but is due almost wholly to the smaller amount of food material stored in the seed. The second

generation from such stunted plants, if grown in good soil, shows little or no diminution in size.

Minor variations due to the inevitable slight differences in the environment of different plants or different parts of the same plant are apparently not inherited. Bean seeds taken from the same plant, for example, vary somewhat in size, due probably to differences in the position of the pods on the plant and in the position and number of seeds in the pod. Johannsen planted the largest and smallest seeds from single self-fertilized bean plants, and found that the beans produced by plants arising from the smallest seeds were just as large on the average as those produced on the plants which came from the largest seeds (Fig. 127, page 341).

Underfed animals frequently bear smaller offspring, and the effect may persist for one or two generations, but ultimately disappears. In underfed silkworms, such a reduction in size persisted for three generations, although the strain had been so injured by starvation that it then died out.

Wherever parental starvation has produced an effect on the size of normally fed descendants, this may be interpreted as a persistent effect of injury to the germ cells, which, as in other cases of such parallel induction, usually "wears off" in future generations.

Kinds of Food.—Variations brought about by a qualitative change in food have not been demonstrated to be truly inherited. The color of the larvae of many butterflies and moths is influenced by the color of their food material, and in a few cases variations in the adult insects have been shown to be due to the same cause. Thus Pictet produced gypsy moths lighter than the normal color by feeding the larvae on walnut instead of oak leaves, their normal food. Two generations of progeny from such light moths were reared on their normal food and were lighter than normal, but descendants in later generations tended to revert to the normal color, showing that the change was apparently a temporary one like the effects of underfeeding.

It has been frequently observed that melanic forms (those which are darker than normal) of some varieties of moths occur more frequently in certain industrial districts of England (the so called "Black Country") than elsewhere. The origin of such melanic types have been referred to the moisture of the area, the darkness of the background on which the moths rest, and most recently to a direct, inherited effect of food, since in manu-

facturing districts the leaves on which the moths feed are covered with soot and metallic salts. Harrison has fed normal moths with metallic salts in an effort to induce melanism, but his experiments do not prove that melanic forms originated in this way. Onslow found that melanism in several such varieties was inherited as a simple dominant to the normal type, and secured evidence that the dark forms were more vigorous than the lighter ones. It has been suggested that for this reason more melanics would survive in the unfavorable surroundings of urban, industrial districts, and that the dark color was probably not produced directly by the environment.

Light.—The variations induced by light of various intensities or colors have also been studied. It has been shown by Kammerer that the non-development of the eyes of cave animals is probably due to the absence of light, since when blind cave animals were exposed to weak light for regular intermittent periods, parts of the normal eye were stimulated to development. From this result it has been argued that the disappearance of the eye in cave animals represents the inheritance of an environmental effect progressively impressed on the germ cells. It also shows, however, that the eye-producing potentiality has been inherited through all the generations of eyeless animals and can be called into full expression by an appropriate stimulus.

Acclimatization.—Natural selection of variations occurring independently of a changed condition probably accounts for many of the adaptations which appear in animals and plants when they are transferred to a new environment. Thus in the South, corn plants have a longer growing season and take longer to mature flowers and seed than corn grown in the North. When such late-maturing southern strains are grown in the North, after several generations they become acclimated to the shorter growing season by maturing earlier than the same strains grown in the South. This has been sometimes regarded as evidence of a cumulative effect of lower temperature and other changed conditions. It is, however, more probably due to natural selection acting on spontaneous variations in growth and maturity rate, for only those plants which mature early will set seed. The others are killed by frost before maturity. Thus each generation is descended exclusively from the earlier maturing plants, and in time the whole population comes to be composed of such plants.

Serological and Other Influences.—The most recent attempts to induce heritable variations have employed new and unusual methods such as immune sera, X-rays, and radium. While it appears possible that some heritable variations have been obtained by these means, it should be remembered that the agents employed are new and not perfectly known, that the experiments to be mentioned are still in progress, and that final conclusions cannot be reached as yet. The methods and results to date have too much interest and significance, however, for the questions under discussion, to warrant their omission.

It has been known for some time that the introduction of foreign substances such as proteins or bacteria into the blood

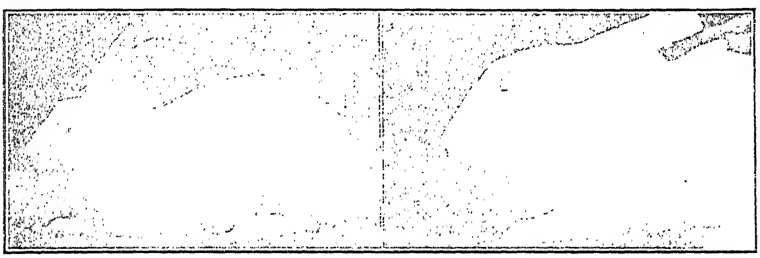


Fig. 107.—Eye defect in a rabbit, descended from ancestors treated with lens antibodies (right); normal albino rabbit (left). (*Photograph at right loaned by Prof. M. F. Guyer.*)

stream of a mammal or bird may induce the formation of *antibodies* in the blood, substances which tend to dissolve, precipitate, or otherwise inactivate the introduced substance (*antigen*) against which they are developed. Making use of this fact, Guyer and Smith caused fowls to develop antibodies against the lens tissues of rabbits' eyes by repeatedly injecting them with the pulped material from young rabbit lenses. The blood of fowls containing lens antibodies was then injected into pregnant rabbits. Among the offspring of mothers so treated several young were found which showed various defects of the eye and of the lens (Fig. 107). These defects proved to be inherited both when the defective-eyed rabbits were bred to their own relatives and when they were crossed to unrelated normal-eyed rabbits. Guyer and Smith believe that a new character (defective eyes) has been produced which acts as a mendelian recessive, although the ratios obtained do not entirely establish the latter point. Similar defects, likewise inherited, have appeared among the

progeny of rabbits which themselves received direct injections of rabbit lens material while pregnant.

The explanation advanced by Guyer and Smith is that the lens antibodies, either directly induced in the blood of the pregnant rabbits or introduced through the fowl's blood, have attacked and injured the lenses of the embryo rabbits, while these were in the body of the treated mother, and that they have also affected the germ cells of some of the embryo rabbits in the same specific way, causing the origin of a new gene for defective eyes. They do not, therefore, regard the experiments as providing evidence that somatic acquirements may be transmitted to the germ cells, but contend rather that both body tissues and germ cells may be affected by the same agency at the same time. This claim differs from that of other experimenters with such parallel induction methods in that it assumes the effects on the germ cells to be *specific* rather than in the nature of *general* injuries such as those induced by poisons.

Another recent set of experiments by Little and Bagg has yielded evidence which suggests the possibility that X-rays applied to mice may have induced the appearance of a new gene, indicating that such an agent may affect a single region of one chromosome.

That the distribution of whole chromosomes may be affected by external agents is made probable by the work of Mavor and of Blakeslee. Mavor was able to induce non-disjunction in *Drosophila* by X-raying the female flies when their eggs were at a critical stage in oögenesis. Blakeslee has succeeded in producing mutations in *Datura* by exposing the parent plants at flowering time to cold and believes that low temperature has induced chromosomal changes in the gametes.

Use and Training.—The changes in animals which are brought about through repeated use, such as the increase in size of much-used muscles, the remarkable habits developed by many animals and plants in response to unusual external stimuli, and the effects of practice and education on mental characteristics in man may all be regarded as typically acquired characters. In spite of a large number of observations and experiments, the question whether such variations may be inherited is still unsettled, although the bulk of the evidence indicates that they probably are not.

Physical Traits.—Many human occupations cause the development of special traits, such as the large muscles of the stevedore,

or the muscular and skeletal changes which follow long-continued habits of posture, as among shoemakers and tailors. These are apparently not inherited. Less clear is the evidence on more ancient and general bodily specializations such as the increased thickness of the skin on the soles of the feet. These thickenings, like callouses, are apparently due to continued pressure; yet the skin of the feet is thickened in the embryo. Is this a heritage from generations of ancestors whose soles became thickened by use?

In the ostrich, also, Duerden has described callouses which develop on those parts of the body which are in contact with the ground when the bird is at rest, or dusting itself. These thickenings seem to arise through use; yet they also appear in the embryo ostrich before hatching, and Duerden believes that through many generations of callous-bearing ancestors, these peculiar adaptive responses have been gradually accelerated in the time of their appearance in development, until now they are present in the embryo, and may, therefore, be said to be inherited. They are interpreted merely as new interrelationships of parts, not as evidence of the formation of new genetic factors. There are many cases similar to these in which the effect of the acquired character on the germ cells is supposed to be a gradual one, requiring many generations for its fulfillment.

Instincts.—If acquired traits are not inherited, what is the explanation of the origin of extremely specialized instincts which the young of so many animals exhibit at birth without training and with no chance for imitation? The young chicken hatched in the incubator and never having seen any older birds, knows how to scratch the ground, pecks at grain and other bright objects, and acts as though it had been taught to do these things. Even more striking instincts among the insects are exhibited but once in life, at the time of mating or egg laying, and appear to be so perfect that one might think they had been learned and practiced. Are these examples of habits which have become hereditary?

When the evidence of history or phylogeny is examined this explanation appears to be very plausible. But in looking for verification of such a conclusion in actual experiment, only negative results and puzzling cases are found. Experimental test of such an hypothesis as Duerden's is, of course, not possible, because it presumes slow change over more generations than

could be observed by an experimenter. The question of the origin of callosities, sole thickenings, and similar effects of use must then remain open, but the question whether the effects of training may be inherited can be put to experimental test with rapidly reproducing animals.

Pavlov, for example, taught mice to come for food at the sound of a bell. The offspring of mice which had been so trained learned the trick more easily than their ancestors. It is probable that this result was due in part at least to the greater general docility of the mice of the later generations, for the original ancestors were wild and shy and hard to teach. With continued inbreeding and selection for docility the wildness of the descendants declined and they were more easily handled and taught. This is given rather as an example of the complexity of the factors involved and the need of caution in interpreting data than as evidence either for or against the heritability of training. Entirely negative results were obtained in a similar experiment on rats by MacDowell, who found that the descendants of rats which had been taught to find their way through a maze required just as much training as their ancestors.

Summary of the Evidence.—A summary of the evidence on the inheritance of acquired characters is best presented by making a direct answer to the three questions proposed at the beginning of this section.

1. Does the response of the parent to a particular set of stimuli predispose the descendants to make the same or a similar response? In the language of Weismann, are somatic acquirements transferred as such to the germ cells? This is the question, "Are acquired characters inherited?" in its narrowest sense. It must be admitted that at the present time it cannot be answered certainly by yes or no. It is evident, however, from the representative experiments and observations cited that the probabilities are decidedly against the inheritance of such somatic acquirements as disease, mutilations, the effects of poisons, malnutrition, variation in food, light, and temperature, and the changes produced by use, disuse, and training.

2. May the germ cells be affected in the same way and at tne same time that the variation is induced in the parent? It is highly probable that such parallel induction does occur, as in general injuries produced by malnutrition, poisons, and similar agencies. The effect of these factors does not generally persist

for more than a few generations and cannot be regarded as truly and permanently inherited. Sometimes, however, as in induced eye defects, it is possible that the tissues of an animal, while these are in a plastic or sensitive stage, may respond in a specific way to a new stimulus such as that provided by the presence of antibodies, and that the germ cells may respond specifically at the same time, with the result that this changed response may be permanently inherited.

3. May new hereditary changes (mutations) be induced by the action of environmental agents? Here the response to an external stimulus is not by the body, nor by body and germ cells together, but only by a specific portion of the germ cell in which the mendelian factors are located. Most experiments, such as the use of poisons to induce mutations in *Drosophila*, have given negative results; but to this general rule possible exceptions must be noted in the case of cold on *Datura* and of X-rays on mice and *Drosophila*. In addition, it is highly probable that several external agencies may influence the chromosomes during maturation, and thereby bring about novel realignments of existing traits, if not actually novel inherited conditions.

Conclusions.—It is safe to conclude, therefore, that the heritability of few or none of the variations which are ordinarily spoken of as environmental has been definitely established, and that it is quite certain that many of them are not inherited. This conclusion is of great theoretical importance, for it indicates that most of the mendelian traits with which genetics deals have probably not originated as direct responses to environmental conditions but in other ways. It means that the rôle of the environment in guiding evolution is probably not that of a creative force, which directly originates the new characters developed by animals and plants. It means, finally, that plant, animal, or human improvement cannot proceed solely or permanently merely by improving the environment of organisms in the hope that these effects will be transmitted to descendants, but must take account of characters originating in other ways, and must proceed by manipulating these characters to man's advantage. It is to this other class of variations that attention will now be turned.

Variations Chiefly Due to Internal Change; Autogenous Variations.—The second major class of variations, as indicated earlier (page 274) is comprised of those which have been called

autogenous; that is, differences which appear not to be correlated with known factors in the environment but to be due to changes or rearrangements within the organism. Most of the traits of which the mode of inheritance is known are of this sort. These have not appeared as the result of deliberate efforts to induce them, but for the most part are of unknown origin. A few variations, however, have arisen under observation in the laboratory or experimental garden, and it is possible to make some statements concerning the manner of their occurrence and the probable location of the internal changes which have preceded their appearance. Autogenous variations are traceable in respect to origin either to the reproductive or germ cells or to the somatic or vegetative tissues. Variations originating in the germ cells may be classified in three categories.

1. Those variations which, although apparently new, prove on analysis to be simply reappearances of older traits or new combinations of factors. To such a reappearing variation the name *recombination* is given.

2. New variations in single factors or genes, such as the sudden appearance of a white-eyed fly in a pure stock of red ones. Such sudden new appearances are called *gene mutations*.

3. Variations arising from changes in the number of chromosomes, such as the appearance of a giant plant with twice the normal number of chromosomes. These are frequently called *chromosome aberrations* or *chromosome mutations*.

From the circumstances of their appearance and their mode of inheritance these types of variation may all be grouped in one category as representing some change or realignment in the reproductive cells.

4. In still another category is to be placed a group of heritable variations which have apparently arisen by sudden changes within some tissue of the animal or plant body other than the reproductive cells themselves. These changes in the vegetative or somatic tissue are referred to under the general name of *bud variations* since they arise most frequently in the growing parts of plants.

Recombinations.—Most of the inherited variations which appear in bisexual animals or plants are due to the segregation or recombination of traits in which the parents are heterozygous (Fig. 108). If a large number of progeny of cross-fertilized plants such as corn, or of rapidly reproducing animals such as mice,

fowls, or silkworms, are observed carefully there will often be found among the progeny characters which were not apparent in the parents, and which cannot be ascribed to environmental factors. Such variations are most frequent in animals and plants known to be hybrids or mongrels, and least so in varieties which have been bred pure for many generations, such as the pure breeds of livestock, or the species of plants which reproduce by self-fertilization. Mongrels are known to be heterozygous in many factors, and pure-bred or self-fertilized types are known to be relatively homozygous. The frequency of such variations, therefore, is usually an index of the relative heterozygosity of

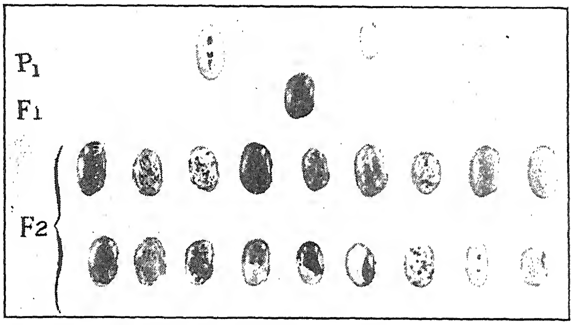


FIG. 108.—Variation due to segregation. The results of crossing dot-eye by white beans (at top). The F_1 beans were all mottled, and in F_2 appeared beans of many different patterns, colors and sizes. (*From Sax.*)

the parents, and their common occurrence indicates that most cross-fertilized organisms are heterozygous in many factors. Many such cases of variability due to segregation and recombination of factors have been cited in previous chapters (Fig. 14, page 29).

That this is the true explanation of much variability is not apparent until breeding tests of the new forms have been made or until the past history and present relatives of the variants have been investigated. In the absence of such data, variations of this type are often thought to represent new characters. Occasionally, for instance, a red and white calf appears in a pure-bred herd of black and white Holstein cattle in which only black and white animals have been recorded for several previous generations. Cole has found that red in such cases is not a new trait but one which may have been present in the stock for many generations. Being recessive, the factor for red may be carried

but not expressed until the chance mating of two heterozygotes provides the opportunity. Such recombinations may characterize many individuals, as in the cross of pea-combed and rose-combed fowls which produce all walnut-combed individuals in F_1; or they may appear with great rarity, as in an F_2 generation from parents differing in three duplicate factors in which the triple recessive has an expected frequency of only one in sixty-four.

Many different types of variation may appear at once, depending on the number of factors in which the parents are heterozygous. The mating of two normal gray mice, for example, may produce as many as sixty-four visibly different types if the parents are heterozygous in six factors. The great increase in variability in the second generation from a cross of two parents differing in size has already been mentioned and it has been shown that this fact is probably due to the segregation and recombination of quantitative factors.

Because of the frequent occurrence of recombination, and the great increase in variations of this sort after crossing, it is not strange that hybridization or crossing should be regarded by some as one of the chief causes of variation and, therefore, of dominant importance in evolution. Although recombination provides a partial explanation as to why variations appear, it tells us nothing about the origin of variations, for the factors which segregate and recombine in new forms have come into being before these processes occur. The real problem is, therefore, to find out how factors themselves originated.

Mutations.—In most cases it is impossible to separate variations due to segregation from those produced by the sudden appearance of new factors, since the past history of most animals and plants cannot be known for a sufficient length of time to eliminate the possibility that the variation has not occurred before and been transmitted as a recessive. It is, therefore, unsafe to assume that any variation which appears in plants or animals of hybrid or cross-bred origin is actually new. A number of variations have arisen, however, in breeding experiments or from pure stocks which have been under close observation, and in a number of cases it is possible to be fairly sure that the characters are new and not due to recombination. Examples of such new variations have been cited in Chap. II. Here it is necessary only to recall such instances as the sudden appearance in a normal

flock of a lamb with bowed, shortened legs which became the ancestor of the Ancon breed of short-legged sheep; or of the finding of a single aberrant flower type in a bed of poppies, from which was derived the present variety of Shirley poppies (Fig. 15, page 31). It is probable that many other variations, such as hornless sheep and cattle, albino animals (Fig. 109), and many distinct varieties of plants (Fig. 110) arose in this way.

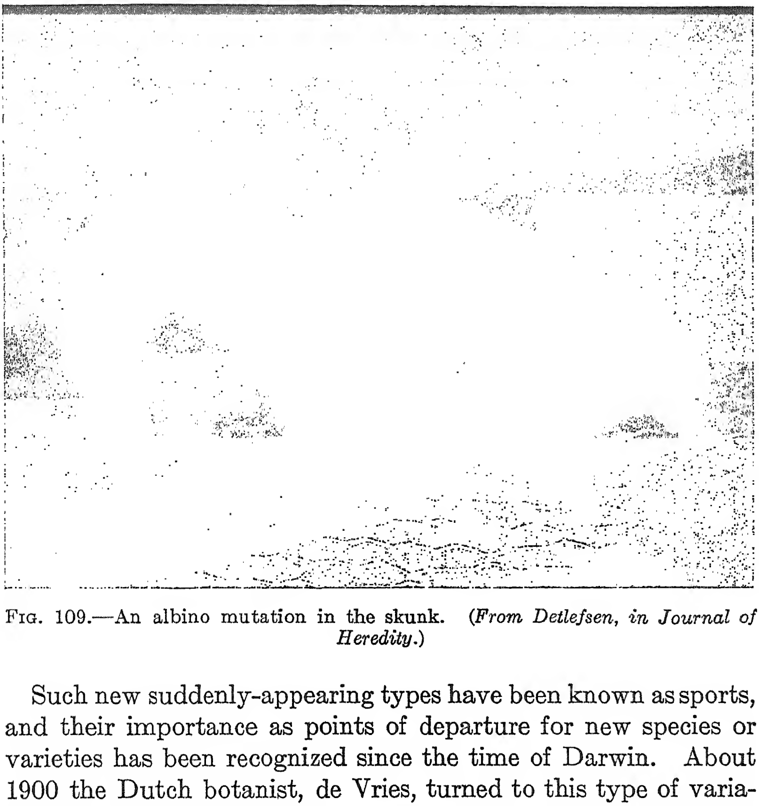


Fig. 109.—An albino mutation in the skunk. (*From Detlefsen, in Journal of Heredity.*)

Such new suddenly-appearing types have been known as sports, and their importance as points of departure for new species or varieties has been recognized since the time of Darwin. About 1900 the Dutch botanist, de Vries, turned to this type of variation as a possible explanation of the way in which new species arose. He found many instances of the discontinuous origin of variations in both animals and plants, and proposed the term *mutation* to describe those cases in which new true-breeding forms appeared suddenly, showed rather wide differences from the parent type, did not intergrade with it, and were apparently not due to environmental changes. He assumed that they were

caused by sudden changes of unknown nature which occurred in the reproductive cells.

It is now recognized that such sudden changes need not necessarily result in large or conspicuous variations, but may affect the minute details of structure, or may cause small or great alterations in all parts of the plant or animal. Moreover, the nature of the changes which take place in the reproductive cells is now somewhat better understood, and it is known that they may result either in the formation of a new gene (gene mutations)

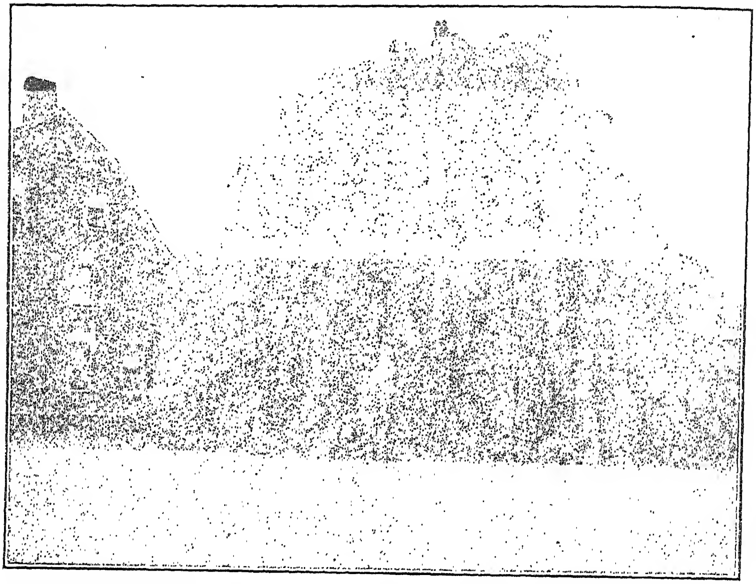


FIG. 110.—The "weeping" form of the European beech, which probably arose from the normal type by mutation.

or in a modification of the number or arrangement of the chromosomes (chromosome mutations).

Gene Mutations.—Knowledge of this type of mutation has been greatly increased by studies on *Drosophila*. Such great numbers of these flies have been reared in the laboratory and examined so carefully that even events as rare as gene mutations have been recorded in relatively large numbers (Fig. 63, page 178). Moreover, the mechanism of inheritance is better known for *Drosophila* than for any other organism, so that when a mutation takes place, the region of the germ cell which has been changed can quickly be determined.

The first mutation in *Drosophila* was discovered by Morgan in 1910. This was a white-eyed fly which appeared in a pure culture of normal red-eyed ones, and proved to be due to a single recessive sex-linked gene. Since that time over 200 mutations have been described and studied, and each has on good grounds been assumed to be due to a change in a single gene, located at a particular point on one of the four chromosomes. A mutation in the narrow sense (gene mutation) in which the term is now commonly used is defined by Muller as "an alteration of the gene." It is a change at some single point in a chromosome. If the change is the first to occur at that point, a new gene arises. More than one mutation may take place at one point or locus, however. Thus several have occurred at the same point at which the original white-eye gene is located, producing true-breeding varieties in which the eyes are cream, eosin, cherry, or other colors. It is certain that the same locus in the chromosome is responsible for these various color types because each type behaves as an allelomorph of every other one, and it has already been learned that allelomorphic genes occupy similar loci in homologous chromosomes. Several such systems of multiple allelomorphs have been found in *Drosophila* and other animals, as, for example, the series of multiple allelomorphs of the albino or the agouti gene in rodents (page 165). Their occurrence indicates that certain regions of the chromosomes are more likely to mutate than others. According to Muller gene mutations have the following peculiarities: They are very rare, although they occur in some loci of the chromosome more frequently than in others; external agents probably do not cause them; they may occur at any time in the life history of the individual; most of them are recessive in their effects, many are deleterious, and some (probably many) are lethal, so that the comparatively few that are found consist of the minority which do not handicap or kill the organism.

It is probable that most mendelian factors have arisen by mutation, and that the inherited variations which characterize existing plants and animals are the remnants of a greater number of mutations which arose in the past, of which only the beneficial or least deleterious survive. In spite of the knowledge as to *where* mutations occur, nothing is known about *why* they do so. Since external conditions do not usually call them forth, it is only possible to conclude that they are in the nature of accidents

in the germplasm. Obviously, they cannot be regularly induced or controlled until more is learned about them, and their origin constitutes one of the most interesting unsolved problems of genetics.

Chromosome Mutations.—The physical basis, although not the cause of origin for one class of heritable variations has been

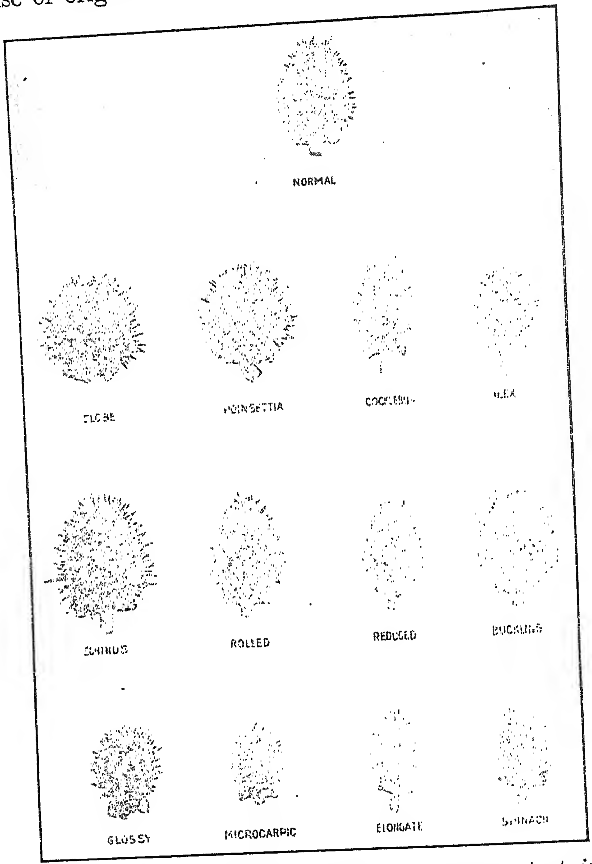


FIG. 111.—The seed capsules of unbalanced chromosome mutants in *Datura* Each mutant type has an extra chromosome in one of the twelve chromosome sets. (*From Blakeslee, in Journal of Heredity.*)

ascertained recently through the combined efforts of cytologists and geneticists. In some plants, for example *Datura*, and the evening primrose (*Oenothera*), and in the fruit fly, *Drosophila*, some individuals have been found which differ markedly from the normal in a number of characters.

In the experiments of Blakeslee and Belling with *Datura*, plants have appeared which differ from the normal in shape of seed capsule, form and arrangement of leaves, height, and other characters (Fig. 111). When crossed with the normal, these do not give simple mendelian ratios. The varying characters are transmitted as a group to certain of the offspring and do not

FIG. 112.—Variation in the evening primrose (*Oenothera*) due to doubling of the number of chromosomes (tetraploidy). At left, leaf and flower stalk of normal *Oenothera lamarckiana;* below it, the seven (haploid) chromosomes of this type. At right, leaf and flower stalk of a mutant form, *O. gigas;* below it, the fourteen (haploid) chromosomes of this mutant. (*Photographs from B. M. Davis, drawings from Sharp.*)

separate and recombine as would be expected if the different traits depended on separate genes. Each of these varied forms has been found to differ from the normal in chromosome number. Normal *Datura* plants have twelve pairs of chromosomes. In one of the mutant types there are eleven pairs of chromosomes and one set of three, indicating that one of the chromosomes has become doubled. Associated with this doubling is a constant

set of plant characters. In each of twelve different mutant types a different chromosome is found to have become doubled, while in other types all of the chromosomes are double, producing a plant with twenty-four pairs instead of twelve. The giant or *gigas* mutant of *Oenothera* and similar variations which have appeared in other plants have been found to have a similar doubling of all of the chromosomes (Fig. 112). Individuals with the usual paired arrangement of chromosomes are known as *diploid* or $2n$ forms; those with four instead of two chromosomes in each set are known as *tetraploids,* and those in which there are three in each set are known as *triploids.*

Chromosome Balance.—Bridges has found that similar conditions may arise in *Drosophila* by chromosome mutation and that abnormal distribution of the chromosomes is accompanied by certain variations in the structure of the fly. It is apparent from the discussion of these variations (page 219) that sex in Drosophila is due to a normal balance between the opposing tendencies of the sex chromosomes and the autosomes, and that some of the mutations in the sexual characters of *Drosophila* are traceable directly to changes in the arrangement or balance of the chromosomes (Fig. 78).

Variations in all parts of the *Datura* plant have been found which are expressions of an unbalanced condition of the chromosomes. In the normal type there are two members of each of the twelve sets of chromosomes. When a particular one of these sets (known as the "globe" set from its effect on capsule form) contains three chromosomes, the seed capsules are globular instead of ovoid, and the leaves are broader and less indented than in the normal. When the globe set contains four chromosomes, the globe characters are exaggerated, and the plant differs still more from the normal. If, however, the extra globe chromosome occurs in a plant in which all of the chromosome sets are doubled (tetraploid), the globe characters are less marked, and the plant is more nearly normal. Apparently, each of the various chromosomes exerts a specific influence on all of the characters, tending to pull them away from the normal, for when any given set contains three chromosomes instead of two, certain very definite changes occur in many characters of the plant, some tending in one direction and some in another (Fig. 113). When all of the chromosomes are present, these opposing tendencies *balance* each other and establish the equilibrium which we call

"normal." If the chromosomes of only one set are increased, their influence is able to outweigh the influence of the other sets in a particular direction; but if at the same time the other chromosome sets, with their opposing tendencies, are also rein-

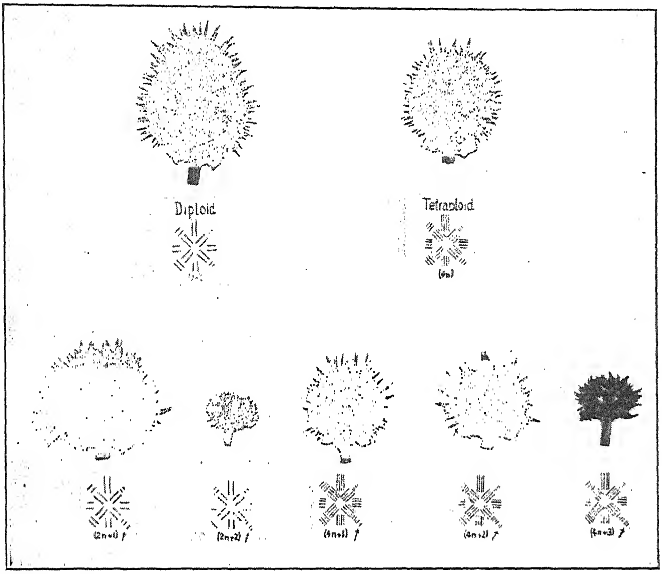


FIG. 113.—Chromosome mutants and chromosome balance in *Datura*, as shown by differences in capsule form. Above, at left, the normal diploid type, from plant with twelve pairs of chromosomes. Below (left) the mutant "globe," in which one set of chromosomes has three members, thus upsetting the normal balance. The effect of this particular chromosome set is evidently to flatten the capsule, for the addition of an extra chromosome to it results in a flatter capsule than the normal. The addition of *two* extra chromosomes (as shown to the right of this) flattens the capsule still further.

Above, at right, a capsule from a tetraploid plant, which has four chromosomes in each set, instead of the normal two. The balance between the twelve sets is thus maintained and there is little difference from the normal in capsule form. The results of the addition of one, two, and three chromosomes to the globe set are shown below. It is evident that the change produced by each additional chromosome is less than it is in a corresponding diploid plant, presumably because the number of chromosomes is greater, the contribution of a single chromosome is less in proportion to the whole, and the balance is therefore less upset. (*From Blakeslee.*)

forced, they tend to counteract the unbalance and restore normal equilibrium.

Variations due to changes in the numbers and distribution of the chromosomes apparently occur more frequently in some plants than do the changes in single points in the chromosome which have been called gene mutations. As in gene mutations,

however, it is probable that only a few of those which occur are found, for any change in these most important parts of the cell upsets the normal balance and may cause deviations which handicap or entirely prevent development. This is especially true where whole chromosomes are involved, for each chromosome probably has an effect on all of the characters of the organism. Thus if the normal balance of the chromosomes is upset by crossing species or varieties with different chromosome numbers, complete or partial sterility frequently results. The sterility of the mule is probably due to differences between the parent species, horse and ass, in the numbers and kinds of chromosomes. When the hybrid mule forms its germ cells, the chromosomes do

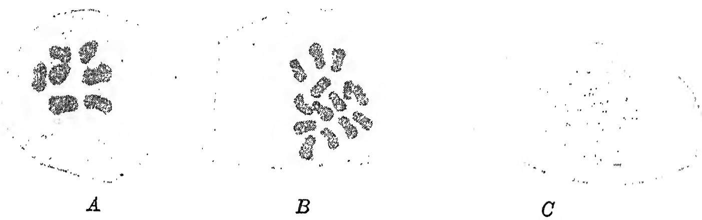


FIG. 114.—Chromosome differences in species of wheat. Reduction division in pollen mother-cells of *A*, *Triticum monococcum*, 7 chromosomes; *B*, *T. durum*, 14 chromosomes; *C*, *T. vulgare*, 21 chromosomes. (*From Sax, in Genetics.*)

not pair or balance properly, and the resulting cells are not able to survive. If a species of wheat, *Triticum vulgare* (Fig. 114, *C*), with twenty-one chromosomes is crossed with another *T. durum* (Fig. 114, *B*) having fourteen chromosomes, some of the hybrids are fertile, but if a species with twenty-one chromosomes is crossed with one with seven chromosomes *T. monococcum* (Fig. 114, *A*) the hybrids form no functional germ cells. A similar explanation probably holds not only for the sterility which frequently obtains in hybrids but for the sterility or lowered fertility found in plants which have unbalanced chromosome sets. In some such cases, for example among the chromosome mutants of *Datura*, many of the germ cells which contain abnormal numbers of chromosomes die or abort soon after they are formed.

The variations discussed above, such as vegetative vigor, general plant characters, sexual characters, and sterility, have great practical and theoretical importance. Many of them defied interpretation until modern cytology applied new methods of research. That the origin of many such variations is now known to lie in chromosome aberrations is at once a not-

able addition to the knowledge of the origin of variations, and a promise of more important advances soon to be made, both in understanding and in application. The great problem of what causes whole chromosomes to become doubled or tripled or to disappear is, like the cause of gene mutations, still unsolved.

Autogenous Variations in Somatic Tissues; Bud Variation.—The variations which have been considered above apparently

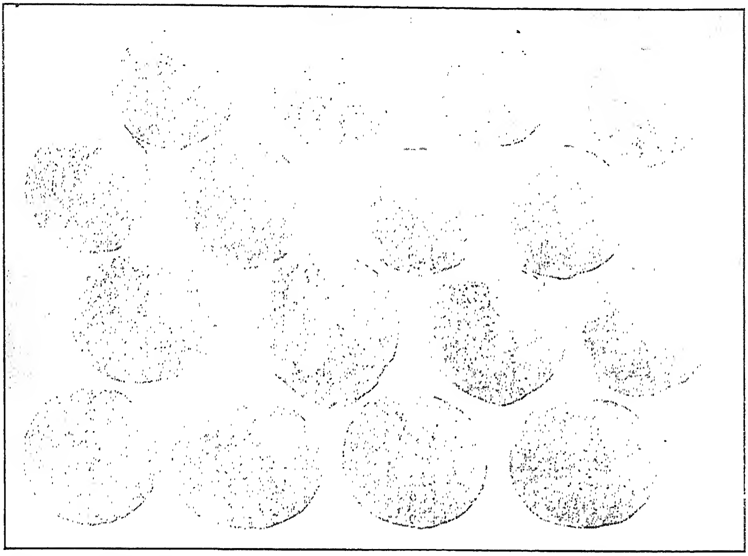


FIG. 115.—Variations, due to bud mutation, in oranges from a single tree. (*From Shamel, in Journal of Heredity.*)

owe their origin to sudden changes which occur in the chromatin of the reproductive cells. Another large group of autogenous variations has been traced to changes in the cells which give rise to the vegetative or somatic tissues. These are most frequently encountered in plants, although it is not impossible that some animal variations may belong in this category. Typical examples of bud variations are those which have taken place in fruit trees which are propagated from cuttings rather than from seed (Fig. 115). In orange trees it is sometimes found that one branch bears fruit which is quite different from that on the rest of the tree. Thus on a tree of the Washington navel variety which bears fruit with rather rough, pebbly skin, one branch was found which bore fruit with smooth skin. When cuttings

from this branch were made, the smooth-skinned characteristics appeared in the descendants, and from these a new smooth variety, the Thomson navel orange, originated. Some varieties of vegetatively propagated plants, such as some of the different strains of

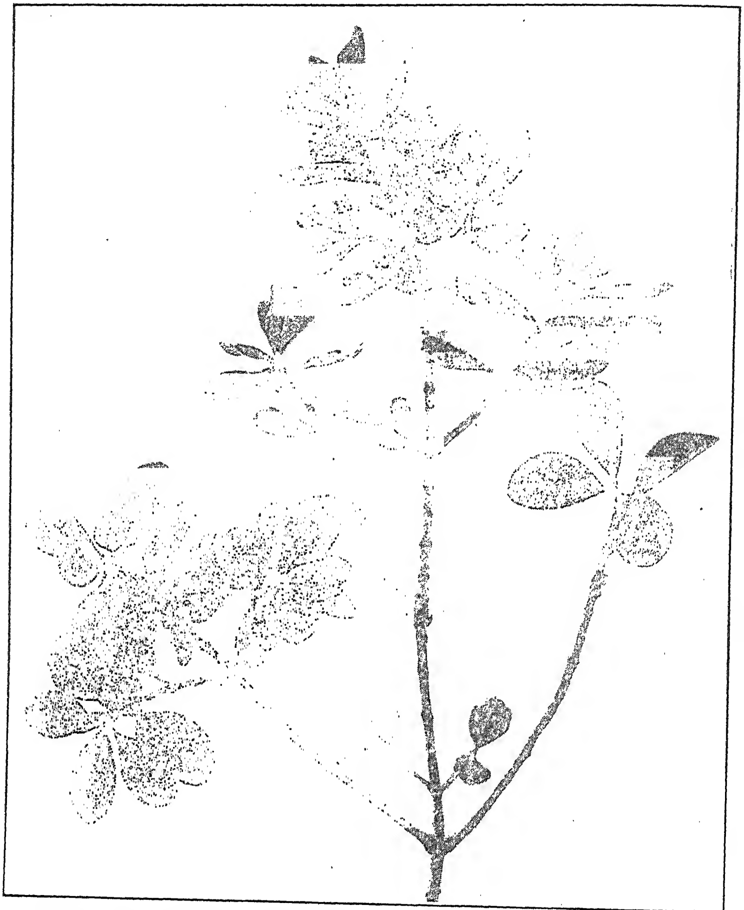


FIG. 116.—Bud variation in a limb of *Euonymus*, showing normal and variegated branches. (*From Shamel, in Journal of Heredity.*)

the potato and of apple and other fruit trees, probably originated in this way.

Bud variations, like germinal variations, may be small or large, and may affect many different kinds of characters. In variegated plants (those which have leaves or flowers of two or more

different colors) a branch or even one or a few leaves may be wholly of one color (Fig. 116). Many examples of this can be seen in the popular foliage plant, *Coleus*. In corn, ears with plain, white seeds may occasionally show seeds with a variable amount of red in the pericarp (Fig. 118). The variations may appear as a scarcely perceptible red stripe or nearly the whole seed may be red. Again, the variation may be one affecting size, as in *Portulaca*. In cultures of this plant, Blakeslee found a dwarf which had apparently arisen from the normal type as a gene mutation, and was found to differ from normal by a single

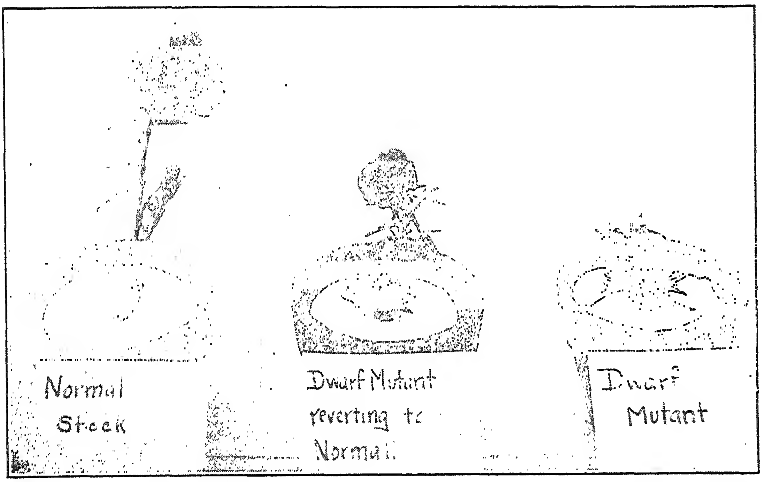


FIG. 117.—Mutation in *Portulaca*. At left, normal plant; at right, a dwarf mutation which is inherited as a recessive; in center a dwarf mutant in which one branch is reverting, by bud mutation, to the normal form. (*From Blakeslee, in Genetics.*)

recessive factor. Rarely a dwarf plant bore a branch of normal size (Fig. 117). Investigation showed that this normal branch arose as a typical bud variation, although it occurred rather more frequently than most mutations.

All of these types of variation have occurred in the vegetative or somatic tissues of the plant, without apparent alteration of the environment. They are strictly inherited either through vegetative or sexual reproduction; that is, they reappear in cuttings taken from the part which shows the variation, and if the variation has affected the parts of the plant from which the reproductive tissues are formed, the new variation may be inherited

through the seeds, in some cases in the same manner as gene mutations. The event that makes one part of a plant differ from the rest probably takes place in the cells from which the varying part arose. Thus if a sudden change occurs in the cell which by division gives rise to a whole branch, all the descendants of this cell might be expected to show the changed condition. If, after the development of the corn kernel was nearly completed, there should occur a mutation from white to red in one cell only, the few descendants of this cell would show the change, and the red variation would be confined to a small area on the kernel (Fig. 118). Exactly what happens in one or a few somatic cells when a bud variation occurs is not yet known, but it is apparent that bud variations, like variations in the germ cells, may be due to several different causes.

FIG. 118.—Somatic mutation in the pericarp of corn. *A*, self-colored; *H*, colorless; *B–G*, variegations. The various types behave as allelomorphs and probably arose by mutations or changes in a single gene in a somatic cell. (*After Emerson, in Genetics.*)

A *gene mutation* may take place in a somatic cell, and give rise to a new factor. In the common four o'clock some varieties have variegated green and white leaves. Occasionally, a wholly green branch arises on such a variegated plant. When seed from flowers on such green branches are sown, the seedlings are green and variegated in the same ratio as though they had come from a parent heterozygous for green. The most probable explanation of this fact is that a gene mutation took place in one chromosome, giving rise to a factor for green, the dominant allelomorph of variegation. All of the cells descended from the one which mutated were then heterozygous, and when reproductive tissue was formed from these heterozygous cells, mendelian segregation took place in a normal way. The same is true of the normal branches which occur on dwarf portulacas (Fig. 117). If self-fertilized seed from flowers borne on such normal branches is sown, the resulting plants are three-fourths normal and one-fourth dwarf. One member of the pair of "dwarf" genes has

probably mutated to normal, and this heterozygous condition obtains in all the cells of the normal branch, including the reproductive cells.

This type of mutation also occurs in animals, as *Drosophila*, and has resulted in such curious *mosaics* as those with an eye of one color on one side and of a different color on the other, or with the tissues of some small part of the body showing characters different from those in the rest of the body.

Somatic Segregation.—Many bud variations seem to be due not to the production of new factors but to segregation of factors during the division of somatic cells, or to abnormal distribution of chromosomes. Bud variations are most frequent in hybrids or heterozygous forms and in such cases it is likely that the change is due to a segregation or combination of factors or chromosomes in a part of the cells.

The best example of somatic segregation is found in the peculiar individuals, part male and part female, which are called gynandromorphs (Fig. 119). These occur with some rarity in *Drosophila*, where they have been carefully studied by Morgan and Bridges. In gynandromorph flies there is a peculiar mixture of male and female parts. Sometimes, for example, the left half of the fly is male and the right half is female. Most of these cases are probably due to abnormal distribution of the sex chromosomes. Thus if in a fertilized egg which starts as a female, one of the sex chromosomes is lost at an early cell division, all the descendants of this cell and the parts which develop therefrom will be male (XO), while the other parts which retain the XX condition will be female. That this is probably the true explanation is shown by the behavior of factors known to be carried in the X chromosomes and in the autosomes. All of the dominant autosomal characters appear in all parts of the gynandromorphs, while the distribution of sex-linked characters is such as would be expected if one of the X chromosomes were missing from the varying, or male-like, part.

FIG. 119.—A gynandromorph of *Drosophila*. The right side of this fly was male; the left side was female. Note differences in the eyes, wings and forelegs of the two sides of the body. (*From Morgan and Bridges.*)

Cytoplasmic Inheritance.—There are a number of other variations in plants whose origin and transmission, while apparently influenced by internal rather than external conditions are, nevertheless, quite different from the cases described above. Most of these are variations in the distribution of chlorophyll in plant tissues. In the common four o'clock, Baur studied one strain which produces plants with leaves and stems irregularly blotched green and white. Only small areas of a leaf may be green or white, or whole leaves and branches may be all green or all white. When flowers from a green branch are self-fertilized, they produce only green plants, which breed true. Seeds from flowers borne on white branches produce only white plants. Seeds from blotched green and white branches produce green, white, and blotched plants. The clue to the cause of this peculiar and irregular variation was found when flowers on green branches were fertilized by pollen from flowers on white branches, in which case only green offspring like the mother were produced; and when flowers on white branches were fertilized by those from green ones, in which case the offspring were all white, like the mother. It was thus found that in whatever way the cross was made, the *offspring always resembled the female parent.* Other cases of this type of *maternal inheritance* are known. A maternally inherited trait is transmitted only through the female line, from mother to offspring, a method quite different from the usual one in which the offspring inherit equally from both parents. Traits which pass through the egg only are evidently located in some substance which only the egg contains. In plants and animals both the male and female germ cells have approximately equal amounts of nuclear material, but only the egg has any significant amount of cytoplasm, and it is consequently to bodies in the cytoplasm of the egg that one may turn for an explanation of maternal inheritance. It is known that in the cytoplasm of plant cells are self-perpetuating bodies called *plastids.* Those which are present in all green tissues normally contain the characteristic plant pigment, chlorophyll, and are known as chloroplastids. The plastids, or their primordia, normally pass into the cytoplasm of the egg and reappear in the progeny. In the variegated four o'clocks, the chloroplastids in the cells of the white areas do not contain chlorophyll. When egg cells are formed from tissue containing colorless plastids, only colorless plastids pass into the eggs, and these by multiplication in

the seedling give rise only to other colorless bodies. Such seedlings become white like the maternal tissue from which they were formed. If the maternal tissue was mixed green and white, the seedlings are of similar character, and the multiplying green and white plastids become distributed irregularly through the cytoplasm, since the division of cytoplasm is not governed by an exact mechanism like mitosis.

The origin and inheritance of such a variation as colorless plastids is thus *cytoplasmic* rather than nuclear, as in other heritable variations. These variations do not conform to the usual laws which govern inheritance through the nucleus, but are similar to those caused by the presence of a microörganism such as that of syphilis in the egg cytoplasm, since the germ cell acts only as a passive vehicle in their transmission from one generation to the next. Cytoplasmic inheritance probably occurs only in a limited number of cases in plants and is not to be considered as a general or widespread method of inheritance or of variation.

In addition to the variations which have been classified in respect to origin as environmental, or as autogenous, there are many which it is at present impossible to classify. Most spotted mammals, for example, show great variability in the amount of black and white in the coat, as Holstein cattle, which vary from nearly all black to nearly all white. In some cases such variations in amount of spotting are known to be governed by genetic factors, but in the guinea pig inheritance plays but little part in determining the extent of white spotting in the coat. Here all variations from large to small white areas appear at random and seem to be due to causes of unknown character which act during early development. In many animals, peculiar accidents of unknown nature may happen at sensitive periods in development and produce such striking variations as headless or tailless chickens, double or twin embryos, and other defects. In the absence of knowledge of what causes such variations they may be ascribed either to some unknown factors of the environment or to spontaneous internal rearrangements.

Graft Hybrids and Chimeras.—There is still another type of variation which cannot well be placed in any of the groups described, but which is important enough to warrant a brief consideration here. This occurs chiefly among plants and is due to the intimate association and intermixture of tissue from

two plants belonging to different species or varieties (Fig. 120). Grafting is a common practice in plant propagation and consists in uniting a bud or branch from one variety with the stem of another so that the two grow together, and a plant with two or more distinct types of tissue is thus produced. These are in contact at only one region, and each maintains its distinct individuality. Occasionally, however, it happens that a bud grows out just at the point where the two kinds of tissue come together and includes cells from each. The branch to which such a bud gives rise thus contains a *mixture of both* and from this branch an entire plant may be produced vegetatively.

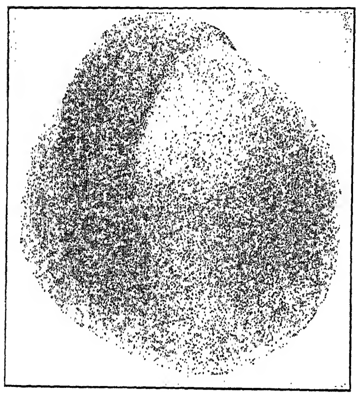


FIG. 120.—A sectorial chimera. Grape fruit with a sector of orange. (*From Journal of Heredity*.)

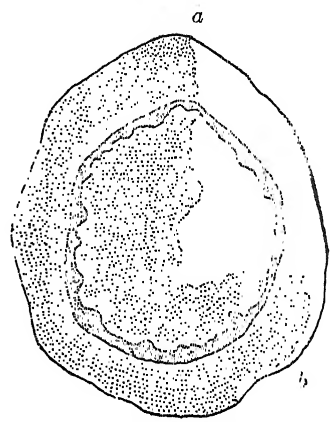


FIG. 121.—Cross section through the stem of a sectorial chimera. A bud arising at *a* would produce a sectorial chimera, but one arising at *b* would produce a periclinal one. (*After Baur*.)

Such a tissue mixture is known as a "graft hybrid" or *chimera*. Sometimes the two kinds of tissue may exist side by side, each occupying a segment of the axis and each maintaining its own individuality. Such are *sectorial* chimeras (Fig. 121). In other cases one type of tissue may completely surround the other, constituting the outermost cell layers and resulting in a *periclinal* chimera. The vegetative characters of such a plant are more or less intermediate between those of its two component species. Winkler produced graft hybrids between nightshade and tomato experimentally and succeeded in obtaining chimeras of both sorts (Fig. 122). In some of the periclinal ones the inner tissue was

nightshade and the outer one tomato, and in others the reverse condition obtained. That the tissues, even in this close associa-

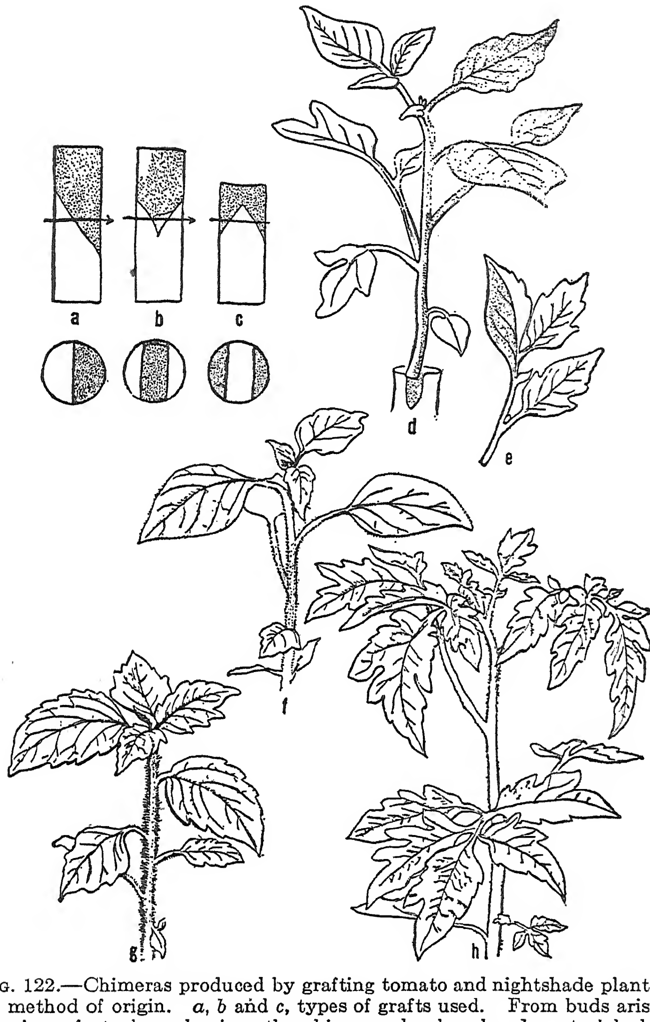


FIG. 122.—Chimeras produced by grafting tomato and nightshade plants, and their method of origin. *a*, *b* and *c*, types of grafts used. From buds arising at the union of stock and scion, the chimeras developed. *d*, sectorial chimera (shaded portion, nightshade; unshaded, tomato); *e*, chimera leaf, part nightshade, part tomato; *f*, nightshade; *g*, periclinal chimera, internal tissue nightshade, epidermal layer, tomato; *h*, tomato. (*After Winkler, from White.*)

tion, kept their distinctive character, was shown by counts of the chromosomes, the nightshade cells always showing their characteristic number of seventy-two and the tomato theirs

of twenty-four. In every case, the fruits and seeds were found to be pure nightshade or pure tomato and resembled those of the species which comprised the inner part of the chimera, a result evidently due to the fact that the reproductive cells arise from the subepidermal layers.

Graft hybrids have arisen from grafts between peach and almond, pear and quince, *Cytisus* and *Laburnum*, and others. They also have been known to originate through a somatic mutation in a cell at the growing point, the tissue developing from this cell becoming mixed with the normal tissue either sectorially or periclinally. Probably some of the plant types which have been called mutations will prove on closer examination to be chimeras of some sort.

Summary.—A number of the ways in which the differences between organisms may arise have now been reviewed. These differences or variations may be due in the first place to differences in the conditions under which the animals or plants live. Any environmental agency which plays an important part in the life of an animal or plant, such as food, temperature, light, water, internal secretions, and the like, must, because of the very responsiveness of living material, act as a cause of variation. Such variations are among the commonest and most noticeable differences which distinguish one member of a species from another.

Whether such direct effects of the environment may account for the origin of inheritable differences has been discussed without arriving at any categorical conclusion. The question as approached here is threefold: (1) whether direct effects of the environment may be transferred as such to the hereditary material and thence become truly and permanently inherited; (2) whether environmental factors may affect parents and descendants at the same time; (3) whether they may induce mutations. The bulk of the evidence on the first question is negative; the second effect probably occurs but has not been demonstrated to be a cause of permanently inherited variations; while the third question, although it has not yet been investigated thoroughly, may at present also be answered in the negative. The experimental evidence, while not conclusive, supports the view that acquired characters are not inherited.

Inherited variations have been regarded, in general, as autogenous or uninduced. The majority of apparently new inherited

characters which are noted are probably *recombinations,* due not to the origin of new factors but to the redistribution of previously existing ones. The heterozygous nature of many animals and plants provides a sufficient opportunity for the appearance of differences of this kind. New heritable variations are thought to be due to changes or rearrangements in the nuclei of the germ cells or, in some cases in plants, to similar changes in the somatic cells. A *gene mutation* is a sudden change in a restricted region of a chromosome resulting in the appearance of a new gene while other germinal variations may be due to changes in the numbers, arrangement, or balance of the *chromosomes.* Variations arising in the vegetative parts may be due to gene mutations or somatic segregation. Finally, some variations are due to agents of unknown origin in the cytoplasm of the egg cells and can, therefore, be inherited only through the mother.

QUESTIONS FOR THOUGHT AND DISCUSSION

112. Is the practice of agriculture more concerned with environmental or with autogenous variations?

113. Light is usually a more important environmental factor in plants than in animals. Explain.

114. What common practice with plants is essentially similar to the ovarian transplantation experiments of Castle and Phillips with guinea pigs?

115. Variations due to the activity of hormones, immune sera, and similar factors of the internal environment are practically unknown in plants. Explain.

116. How do you reconcile the fact that there has been found to be a close relation between the degree of development of the ductless glands and various bodily traits, such as size, hairiness, and pigmentation, with the theory that these traits are produced by genetic factors?

117. If a given organ produces substances which tend to inhibit the development of that type of organ in the body (as the work of Guyer and Smith suggests), of what importance may this conception be in helping to explain the phenomena of development and regeneration?

118. If members of a white-skinned race are exposed to bright sunlight, their skin is darkened or "tanned." Races native to regions of bright sunlight, like negroes in the tropics, are genetically dark-skinned. How would Lamarck explain the dark skin of such races? How would Darwin?

119. Why is it that qualities like immunity or diseases like syphilis may not be transmitted through the male?

120. If acquired characters are not inherited, how do you think it has come about that plants and animals are so well adapted to the conditions under which they live?

121. How could you explain the possession by animals of highly developed instincts which the individual itself has had no opportunity of acquiring, assuming (1) that acquired characters are inherited; (2) that they are not?

122. What advantages and what disadvantages to human society would result from the inheritance of acquired characters?

123. Most mutations are thought to be harmful rather than helpful to the organism in which they appear. Why?

124. If a recessive mutation appears in the formation of a gamete, under what conditions will it come to expression in an individual?

125. From an examination of the chromosome maps of *Drosophila* do you think that mutations are equally likely to occur in all regions of the chromosome?

126. Similarity between individuals has generally been ascribed to descent from a common ancestor. In what other way might such similarities have arisen?

127. All the chromosome mutations of *Datura* may be obtained from the offspring of a triploid plant. Explain.

128. The cells of tetraploid plants are usually larger than those of diploid (normal) ones. What explanation can you suggest for this?

129. It is claimed that some types of plants which are propagated vegetatively in time "run out" or fail to maintain their original character. To what might this change be due?

130. If two apple trees of the same variety differ markedly in their yield, and buds taken from the better one consistently produce better yielding trees than buds taken from the poorer one, what conclusion would you draw? If buds taken from these two trees produce trees which are essentially similar in yield, what conclusion would you draw?

131. If continuous selection within a variety of potatoes is followed by increase in yield, what conclusion would you draw?

132. There are persons with one brown eye and one blue one. How do you explain this?

133. Bateson has reported a *Bouvardia* plant in which branches arising from the roots produce flowers of a different sort from those borne on the ordinary stem branches. What explanation for this can you suggest?

134. Grafts between nightshade and tomato can be made, but these two species will not cross with each other. What explanation can you suggest for these facts?

135. How would you determine whether a given variation is due to a mutation or to the segregation of genetic factors?

136. With what type of autogenous variations are plant breeders chiefly concerned?

137. A plant or animal will usually respond to changes in the environment by changes in structure or function which are advantageous to itself. How do you explain this?

138. Most mutations are recessive in their inheritance and many are of the nature of abnormalities. How, then, can the progressive evolution of the plant and animal kingdoms be explained?

139. Which do you think are more important in producing evolutionary change, those variations which are due to segregation and recombination of factors, or those which are due to mutation? Explain.

PROBLEM

Note.—In *Datura*, Blakeslee has found twelve mutants, each of which is due to the presence of three chromosomes instead of two, in one of the twelve sets. The mutant "Poinsettia" he finds to be due to the presence of three chromosomes in the set which carries the genes for purple and white flower color. Letting A stand for purple and a for white, there may thus be four kinds of Poinsettia plants: AAA, AAa, Aaa (purple), and aaa (white); and three kinds of normals, AA, Aa (purple), and aa (white). The formation of female gametes here takes place much as it did in the non-disjunctional females of *Drosophila.* In the pollen grains, however, *no grains with the extra chromosome are able to live,* apparently on account of the upset balance between the chromosome sets. All pollen grains formed by Poinsettia plants, therefore, are A and a, while the eggs may be A, AA, Aa, a, or aa. The female gametes formed by an individual with the genotype AAa, for example, are two A, two Aa, AA, and a. This may perhaps be worked out most readily by writing the genotype thus: $\frac{A \diagdown\diagup A}{\diagup a \diagdown}$ and making the three possible reduction divisions, AA and a, Aa and A, and Aa and A. If these were male gametes, the AA and Aa types would not develop, and the survivors would be two-thirds A and one-third a.

242. What will be the ratio of purple-flowered to white-flowered plants in the normal ($2n$) offspring and in the Poinsettia ($2n + 1$) offspring from the following crosses?

Female parent × male parent		Female parent × male parent	
AAa	AAA	Aaa	AAA
AAa	AAa	Aaa	AAa
AAa	Aaa	Aaa	Aaa
AAa	aaa	Aaa	aaa
AAa	AA	Aaa	AA
AAa	Aa	Aaa	Aa
AAa	aa	Aaa	aa

REFERENCE ASSIGNMENTS

83. Give an account of an experiment (not mentioned in the text or problems) which has established a definite relationship between some specific environmental agency and the occurrence of variation in plants or animals.

84. Distinguish between *hormones*, *auximones*, and *vitamines*.

85. Give an account of the life and work of Lamarck.

86. Give an account of the views of Herbert Spencer on the inheritance of acquired characters as applied to the evolution of human society.

87. Give an account of the life and work of Weismann and state his important contributions to genetic theory.

88. What was Samuel Butler's mnemonic theory of heredity?,

89. Describe and criticize the experiments of Brown-Séquard on the inheritance of induced epilepsy in guinea pigs.

90. Give an account of the work of Kammerer on the inheritance of acquired characters in amphibia.

91. Name some important types of cultivated plants, or domestic animals, other than those mentioned in the text, which have arisen by mutation.

92. Give an account of the mutations found by de Vries and others in *Oenothera lamarckiana*, with explanations which have been offered for their origin.

93. Give an account of the mutation theory of evolution proposed by de Vries.

94. What is meant by *orthogenetic* variation?

95. What bodies in the gametes other than the chromosomes have been suggested as carriers of inheritance?

96. Give the derivation of the following terms and explain why each is appropriate:

Autogenous	Tetraploid
Mutation	Chimera
Somatoplasm	Periclinal
Triploid	Sectorial

CHAPTER XII

THE APPLICATION OF GENETICS IN PLANT AND ANIMAL BREEDING

The knowledge of inheritance which has been gained under the stimulus of the mendelian discovery has shown that heredity is an orderly process with certain constant characteristics. The inherited traits are transmitted according to laws which may be stated mathematically, and the results in particular cases may be predicted from past experience. The chief of these laws or principles are (1) those which affirm the existence of paired units (factors or genes) which have a high degree of constancy and which *segregate sharply* from each other in inheritance; and (2) those which define the ways in which these units are distributed among the progeny in bisexual reproduction. Assortment of units either independently or when linked with one another is a *measurable* process and conforms to principles of very general application. These principles are the foundation of the science of genetics, for they not only explain the mode of inheritance in most animals and plants but have thrown much light on the mechanism of the process.

Methods of Practical Application.—An understanding of general principles is prerequisite to the manipulation or control of any natural process, and thus to the application of scientific facts and theories to practical life. Knowledge of the principles of inheritance has now arrived at the point where the animal and plant breeder may begin to apply them. Traits, the inheritance of which is known, may be eliminated from the population or may be made to appear in combination with other traits. Manipulation of this sort is limited by the actual knowledge of the specific traits involved, and this must be gained through experiment; but where such knowledge is extensive, as, for example, with respect to the coat characters of rodents or the eye and wing characters of *Drosophila*, the breeder is able quickly to produce varieties with any desired combination of traits. This does not mean, however, that man is now able to *control*

inheritance in the sense that he may dictate what characters shall appear. Control in this sense implies the power to originate new heritable variations, and man has not yet acquired this power, although there is evidence that such control is not an unattainable ideal. The inherited variations with which the breeder works appear to originate by chance or through the operation of forces of which he is at present ignorant. Mutations in the direction of desired types are still only lucky events which occur with great rarity.

Direct Application.—In spite of the lack of the power to originate particular traits, the ability to manipulate or guide inheritance has produced several results of distinct value to the breeder. One of the first demonstrations of the usefulness of the newly discovered mendelian principles was given by the English investigator, Biffen, to whose breeding work with cereals reference has already been made. The following description of the problem and of Biffen's solution of it is quoted from Punnett's "Mendelism."

Taken as a whole, English wheats compare favourably with foreign ones in respect of their cropping power. On the other hand, they have two serious defects. They are liable to suffer from the attacks of the fungus which causes rust, and they do not bake into a good loaf. This last property depends on the amount of gluten present, and it is the greater proportion of this which gives to the "hard" foreign wheat its quality of causing the loaf to rise well when baked. For some time it was held that "hard" wheat with a high glutinous content could not be grown in the English climate, and undoubtedly most of the hard varieties imported for trial deteriorated greatly in a very short time. Professor Biffen managed to obtain a hard wheat which kept its qualities when grown in England, but in spite of the superior quality of its grain from the baker's point of view, its cropping capacity was too low for it to be grown profitably in competition with English wheats. Like the latter, it was also subject to rust. Among the many varieties which Professor Biffen collected and grew for observation he managed to find one which was completely immune to the attacks of the rust fungus, though in other respects it had no desirable quality to recommend it. Now as the result of an elaborate series of investigations he was able to show that the qualities of heavy cropping capacity, "hardness" of grain, and immunity to rust, can all be expressed in terms of mendelian factors. Having once analysed his material the rest was comparatively simple, and in a few years he has been able to build up a strain of wheat which combines the cropping capacity of the best English varieties with the

hardness of the foreign kinds, and at the same time is completely immune to rust. This wheat has already been shown to keep its quality unchanged for several years, and there is little doubt that when it comes to be grown in quantity it will exert an appreciable influence on wheat growing in Great Britain.

A number of similar instances of the direct application of simple mendelian principles to animal and plant breeding could be adduced, but to quote at length would be to overemphasize the importance of this method of application. It must be remembered that most of the economically valuable varieties of cattle, horses, hogs, and fowls, and many of the improved strains of crop and garden plants, have been produced by practical breeders who worked without a knowledge of the more recently discovered principles of mendelian heredity. There can be no question that these men, to whom the farmers of today owe such a debt of gratitude, did recognize certain rules as inherent in their own stock, but since they did not discover laws, they could not generalize or shorten the process of improvement for breeders of other forms. The perfecting of Marquis wheat, for example, which now covers 15,000,000 acres in Canada and the northern United States, involved no direct or simple application of mendelian principles but began with the lucky discovery of three superior plants, followed by long, persistent selection, crossing, and testing, which finally resulted in a great triumph in plant breeding. Luther Burbank, whose work in producing improved varieties of plants has received so much popular attention, has been able to accomplish many remarkable feats in breeding without having recourse to mendelian methods or principles. In considering the applications of genetics, therefore, one must be careful not to claim too much for the direct use of the new science. It has shown its first fruits of value in direct application, and the future for even this limited type of usefulness is bright, although in view of the remarkable achievements already wrought by practical breeders the addition of one new tool cannot be expected to revolutionize the art of breeding.

Indirect Applications.—There is a wider field, however, in which a knowledge of genetics may be useful to the breeder. In very general terms this lies rather in an appreciation of the principles of genetics than in an application of specific facts already

obtained, and it is in this direction that it makes its greatest appeal to the intelligent breeder. The achievements of the past, although remarkable, have been gained only through great pains extended over long periods. They owe much to the rare insight and persistence of a few exceptional men and have often been begun with, and aided by, sheer good luck. The well known successes are amply balanced by less known failures. The knowledge that heredity is a force of great constancy and regularity may be expected to remove some of the element of chance in those cases in which its operation is understood. The successful breeder has often been unable to explain the cause of his good results and has, therefore, failed to duplicate them. He has been puzzled by the sudden reappearance of ancestral traits, the occurrence of unusual variations, or the appearance of what seemed to be evidence of a taint in the blood of his pure-bred animals. Without a knowledge of the principles of inheritance he has drawn false inferences from such facts. Genetics has already been able to provide an explanation of many results which have been ascribed to "telegony," "maternal impressions," "atavistic taint," and the like.

A knowledge of the general principles of inheritance may thus provide an explanation of facts already known, and may thereby shorten the time and labor involved in breeding operations, may add an element of certainty and an ability to realize predictions in some cases, and may increase the confidence of the breeder and his power over his living materials.

There are, however, other useful rules, principles, and practices in breeding operations which have not yet been discussed and which are of especial value in practical breeding. At one time these appeared to form a group apart from the basic principles of heredity, but now it is known that such matters as the results of selection, the existence of so-called pure lines, and the consequences of various systems of mating (such as inbreeding), all produce their results by virtue of the operation of the mendelian mechanism of heredity. It is in the understanding of this last-named group of results, which have been remarkably clarified by recent work in genetics, that the breeder will find the greatest stimulation and help in solving his problems. All of these applications depend on a thorough understanding of the elementary principles involved, and the rest of this chapter will consequently be devoted to a discussion of the practical use of these principles.

Inheritance of Economically Important Traits.—Most of the characteristics of domesticated animals and plants which are of direct economic importance are extremely complex. Milk production in cattle, egg production in fowls (Fig. 123); size, conformation, meat and wool characteristics in farm animals; and yield, rate of growth, form and quality of fruits, disease resistance, and other traits which determine the value of cultivated plants, depend on many factors, both environmental and inherited. The relative parts played by these agencies are still unknown in many cases, and where such a condition obtains, it is obvious

FIG. 123.—A valuable variation in the domestic fowl. At left, a purebred Rhode Island Red fowl which laid 336 eggs in 365 days; at right, a mongrel hen which, like the wild ancestors of the fowl, laid only 50 eggs in a year. (*Photograph of purebred bird from Storrs International Egg Laying Contest, courtesy Prof. W. F. Kirkpatrick.*)

that the details of the inheritance of these traits can be but imperfectly known. That genetic factors do play an important part in the determination of all these characteristics can hardly be questioned, for strains or races of undoubted superiority which breed fairly true in one or another of these respects have been isolated. In a few cases superiority in some specific trait has been found to rest on a relatively simple genetic basis. The most striking examples of this are to be found in disease resistance in plants. The experiments of Biffen (page 329) which showed that the difference between resistance and susceptibility to wheat rust (*Puccinia graminis*) may be due to a single factor have already been cited. In this case susceptibility is dominant, and

since recessive resistant types breed true, the isolation of such a type is a relatively simple matter. The size and habit of the plant is also frequently dependent on a single factor, as, for example, the differences between climbing and bush habit in beans, and between standard and dwarf vines in tomatoes. Pearl and others have shown that the inheritance of winter egg production in fowls, which economically is the most important part of the annual cycle of fecundity, may be explained by the operation of two factors. Such characters lend themselves immediately to the manipulation of the breeder.

Lethal Factors.—Factors which affect development, in some cases so profoundly as to prevent it entirely, are obviously of great practical importance. Such are the so-called *lethal* factors. Those which hinder or prevent chlorophyll development and produce white or albino seedlings in corn fall in this class, since such plants are unable to develop beyond the seedling stage. Another lethal factor in corn affects the seeds, causing them to abort or become otherwise defective and incapable of germination. From a cross of two normal plants which are heterozygous for a factor of this sort, ears are produced which contain normal and defective seeds in the ratio of three-fourths normal to one-fourth defective. Lethal factors are probably responsible for some of the mortality which occurs among the unborn embryos of some animals, and in animals such as cattle, swine, and chickens, where the survival of embryos is a factor of great economic importance, the losses caused by the segregation of lethals may become considerable. Among Dexter-Kerry cattle, as bred in England, it is common for cows to abort about two months before term, and to produce monstrous or deformed dead fetuses known as "bulldog" calves. From certain matings such calves are produced with a frequency approaching 25 per cent of the total, and it is probable that the deformity is caused by a single recessive factor, the primary effect of which may be an alteration of one of the glands of internal secretion, which in turn produces the defects of the skeleton and other parts, and causes death before the normal period of birth. In swine it has been found that only about two-thirds of the embryos which begin their development live to be born, and while the condition of the mother may account for some of this mortality, it is quite possible that here, as with the mouse embryos which die before birth (see page 114), lethal factors

may be responsible for an important part of the mortality. The greatest losses from the death of embryos occur among poultry, for here the mortality may reach 50 per cent or more of the total number of embryos which begin their development. After allowing for environmental causes of death during incubation, a large unexplained mortality remains, which there is some reason to believe is caused by the segregation of lethal factors.

Since factors with such serious effects are always recessive in inheritance, and since their presence usually cannot be distinguished in heterozygous individuals, ordinary methods of selection are powerless to eliminate them, but because of the knowledge of their mode of inheritance other methods of dealing with them can be prescribed. These are treated more fully under the later discussion of inbreeding.

Vigor.—Most of the factors affecting characters of importance to the breeder, however, are not inherited in as simple a fashion as this. It has already been shown (Chap. X) that quantitative characters, such as size, are controlled by multiple factors. This is true also of general vigor and rate of growth, which are resultants of variation in many characters which may show independent inheritance. Direct data on this point are difficult to obtain for the larger farm animals, but Wright has shown from an analysis of experiments with guinea pigs extending over nearly twenty years that the factors affecting general vigor, growth, and reproduction are numerous, separable, and probably specific. Thus, resistance to tuberculosis, although inherited, is not correlated with rate of growth or fecundity, nor is rate of growth correlated with the mortality rate of new-born young. All evidence points to the presence of many separable factors affecting such general characters as these.

Examples from Animal Breeding.—The traits of greatest economic importance to the breeder of dairy cattle, to take an important example, are (1) the quantity of milk produced, and (2) the quality of milk, particularly with respect to the proportion of butterfat which it contains. There is ample evidence that heredity plays an important part in determining both of these traits, for well-marked breed and varietal differences in milk yield and butterfat percentage exist, and within the breeds occur families or lines characterized by high milk production or high butterfat production (Figs. 124 and 125). In spite of their expression in only one sex, Gowen and others find that these

traits are inherited equally from both sire and dam. Direct experimental evidence on the inheritance of milk yield and fat percentage is not abundant. When parents diff ring in these respects are crossed, as for example when Holstein-Friesian cattle, which produce much milk with a relatively low proportion of fat, are crossed with Jerseys or Guernseys, which produce less milk with a higher proportion of fat, the F_1 cows are intermediate between the parents in both traits. The average amount of milk produced by the F_1 cows is nearer to the high-producing

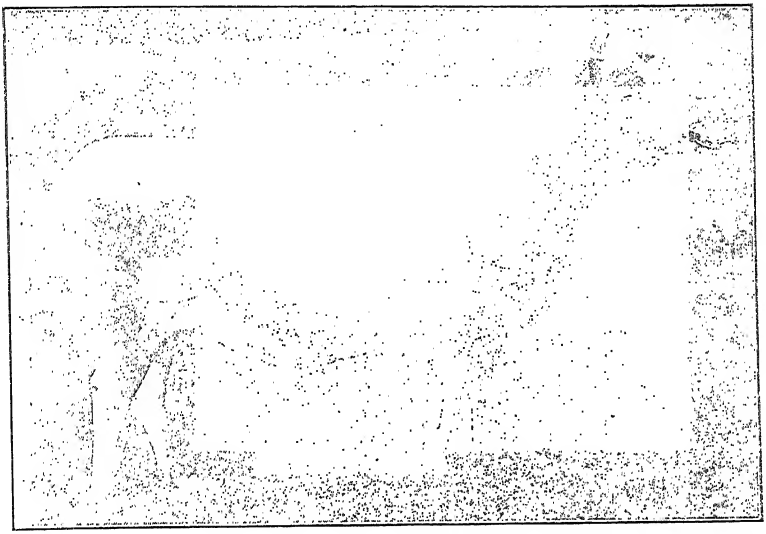


FIG. 124.—A famous Jersey sire, Fauvic's Prince 107961. A first-prize winner himself at the National Dairy Show and a sire of prize winners. Notable for his unequalled record as a sire of daughters with high milk and butter records. (*Courtesy of A. V. Barnes.*)

parent, while the average fat production is somewhat nearer to the lower parent. Gowen believes this is due to the partial dominance of factors for high milk yield and low fat production. Data from segregating generations (F_2 and back-cross) are not available in sufficient quantity to allow an estimate of the number or mode of inheritance of the factors involved, but it is probable that both traits are influenced by multiple mendelian factors. Milk production is known to be influenced also by other genetic factors affecting size, rate of growth, structure, and function of reproductive organs, and by environmental conditions

such as diet, disease, and sunlight. The breeder of dairy cattle may confidently expect specific help from genetics in the future, but results obtained up to the present have little economic value beyond the assurance they give that this important prodlem may be attacked by the same methods which have been successful in solving simpler ones.

The application of genetics to the problems of the breeder who is working to improve the type or conformation of his livestock,

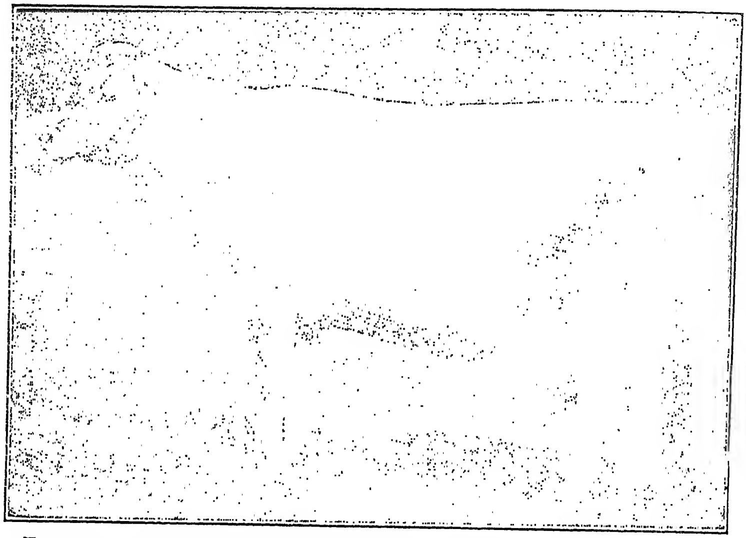


FIG. 125.—A result of successful breeding. Fauvic's Star 303018, one of four Medal of Merit daughters of Fauvic's Prince. She produced in one year 20,616 pounds of milk (a world's record for the breed) and 1005.9 pounds of butter-fat, and is one of three daughters of her sire to produce over 1,000 pounds of fat in one year. (*Courtesy of A. V. Barnes.*)

if only specific applications founded on a knowledge of the inheritance of the details of structure are considered, is also a matter for the future. The inheritance of gross variations, such as the presence or absence of horns, or the short legs characteristic of Dexter-Kerry cattle, may, to be sure, be explained in simple mendelian terms, but these, in general, are not the kinds of variations with which the practical breeder deals. He is often concerned with differences of conformation which are so small that only experienced judges can detect them, and deals not with a few but with many such characters at once. It is prob-

able that many minor variations of this sort are non-genetic, or are due to complex combinations of genetic and developmental factors which occur with great rarity. An exact statistical study of the interrelationships of parts must precede a genetic analysis, which can produce specific information only when well-contrasted hereditary differences appear.

Examples from Plant Breeding.—The most important characters of crop plants, such as yielding ability, quality, and disease resistance, fall in general into the same category with vigor and growth in animals, except that more specific information is at hand. That such characters depend on mendelian factors obeying the usual rules of inheritance has been more clearly demonstrated for some plants than for farm animals in general, possibly because the number of factors affecting the plant characters is fewer, but more particularly because methods of isolating pure types, such as self-fertilization, may be employed with most plants, whereas the higher animals reproduce only by cross-fertilization.

In corn, for example, which is the most important single crop plant in the United States, yield is very definitely influenced by genetic factors. Crosses between plants differing in length of ear, diameter of ear, and weight of seed, together with other size characters such as height of plant and number of nodes, have shown that these traits are all heritable and are apparently determined by a series of multiple factors. Indeed, a study of the inheritance of these quantitative characters in corn by East was among the first thorough investigations of the hereditary transmission of size traits, and placed the multiple-factor hypothesis on a firm basis. The work of East, Jones, and others on heterosis as a means of increasing yield in corn holds great promise of definitely raising the productivity of this crop.

The inheritance of the number, shape, and texture of tobacco leaves, and the synthesis by Hayes, East and Jones, and others of a new type of tobacco through the combination of a number of desirable traits following a cross, is an excellent example of the application of mendelian conceptions to practical breeding. None of the tobaccos grown in New England were satisfactory in all respects, but two varieties, Broadleaf and Sumatra, possessed between them the desired qualities. Broadleaf has a relatively small number of leaves while Sumatra has relatively many. A list of the other leaf characteristics of these two

types, together with the combination desired by the tobacco growers, is given in the following lists (from Jones):

Broadleaf	Sumatra	Desired Type
Large leaf	Small leaf	Medium-sized leaf
Narrow tip	Round tip	Round tip
Drooping leaf	Upright leaf	Upright leaf
Leaves close	Leaves apart	Leaves close
Texture coarse	Texture fine	Texture intermediate
Leaves thick	Leaves thin	Leaves intermediate
Flavor good but strong	Flavor none	Flavor intermediate
Yield high	Yield low	Yield high

These two varieties were crossed, and all their traits showed distinct segregation in the F_2, though in each case it was of the more complex or multiple-factor type. Selection among the F_2 and six subsequent inbred generations was successful in isolating a new type, Round Tip, which combines these various desirable traits and bids fair to be a distinct contribution to tobacco culture (Fig. 126).

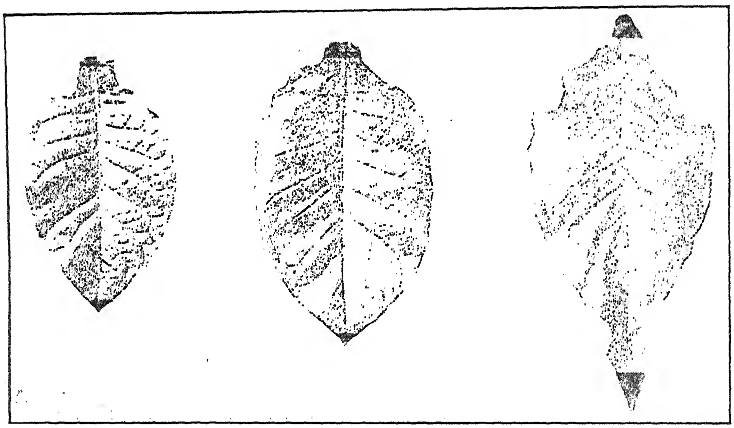


Fig. 126.—Round Tip tobacco, a new variety produced by crossing and selection. A leaf from each of the parent types, Sumatra (left), and Broadleaf (right). A leaf from Round Tip in the center. (*From Jones.*)

Yield in many other crop plants has been found to be inherited, and although this usually occurs in a a rather complex fashion, more extensive experimental work will doubtless result in the manipulation of these economically important quantitative plant characters much as in simpler traits now.

In general, then, the exact mode of inheritance of the more valuable economic traits of animals and plants remains to be

determined, and the contributions of genetics to specific breeding problems which depend on such knowledge have not been extensive. It should be remembered that the technique of investigation and the general rules of inheritance have now been brought to the point where they can be made to produce results with all sorts of characters, and that wherever any material, however difficult, has yielded at all to genetic analysis, it has been found to fall within the range of the mendelian explanation.

Selection.—The specific applications of genetics, as briefly discussed above, depend on a knowledge of the inheritance of economically valuable traits and on a familiarity with mendelian principles. Practical breeders have for generations worked without such knowledge and have in many cases achieved valuable results. The chief method of the progressive breeder has been, and continues to be, *selection* or the choice, for breeding, of those plants or animals which approach most nearly to the type desired. Such selection has been based almost wholly on the *appearance* of individuals or groups, without regard to ancestry, progeny, or degree of relationship of the individuals selected. Since the introduction of pedigree-breeding methods, however, ancestry has become to some extent one of the criteria of selection, although in general farm practice the old methods prevail.

As a means for changing the character of a population, selection has usually been applied to characters which show quantitative variation for it is only in connection with such characters that it is a necessary recourse, since single recessive traits may be fixed in the population by a single selection. With variable traits such as size, shape, quality, pattern, and the like, in which the extremes do not usually breed true, the breeder is forced to depend on the slower process of selecting individuals which show slight variations in the desired direction.

Remarkable results have been achieved by this method both with domesticated animals and plants, and a vast amount of practical information has been obtained. The breeder has found that some characters yield readily to selection, and that progress is rapid up to a certain point, after which it becomes ineffective. Other characters have shown no change under the same methods. Similar systems of selection have given different results, and in the absence of a general explanation of the manner in which selection accomplishes its aims, or fails to do so, there has been confusion and disagreement over the efficacy of the

process. Within the last two decades, however, the effect of selection has been carefully investigated, and a general explanation of its operation and results has been offered in mendelian terms.

Pure Lines.—The first experiments in which both the results and the interpretation marked a distinct advance in our understanding of selection were made by the Danish botanist, Johannsen, the results of which were published in 1903. Johannsen studied the effect of selection on the weights of individual seeds of the Princess bean. The bean plant, like the pea, is normally self-fertilized, the stamens and pistil being enclosed within the corolla and the ovules fertilized by pollen from the same flower. Variations in the characters of such a plant are, therefore, not due to crossing and subsequent segregation of factors. Johannsen found that the bean seeds harvested from many plants of the same variety grown under the same conditions ranged in weight from 25 to 85 centigrams each, with an average of about 50 centigrams. From such a mixed sample a heavy bean (80 centigrams) and a light one (30 centigrams) were selected and planted. The seeds borne on the plant from the heavy seed were then found to average about 65 centigrams, while those from the light plant averaged about 45 centigrams. Selection in this case produced an increase of 15 centigrams and a decrease of 5 centigrams in average weight. It was effective.

From this same random sample nineteen beans were selected, each from a different plant. These were planted and the beans from the resulting nineteen plants were harvested separately. The beans from each plant varied in weight. From the progeny of *each mother plant*, the lightest and the heaviest beans were selected. The plants grown from the lightest and from the heaviest beans from the *same mother plant* were found to produce seeds of the *same average weight* (Table XVIII). Selection among the seeds of the *same plant* was *not effective* (Fig. 127).

Johannsen's explanation of this apparently contradictory behavior was quite simple. Beans are self-fertilized. This means that all the descendants of a single plant have the same heredity, in this case the same factors for seed size. There are no hereditary variations which may be isolated by selection, and selection is, therefore, ineffective. The variations in seed weight which appear among the beans on a single plant are environmental and not inherited, and are probably due to varia-

tions in the placement of the seeds, number in the pod, size of the pod, or other factors. But in the first experiment mentioned, the plants were descended from different parents, and differences in weight were due to genetic factors in addition to other minor environmental influences. A field of bean plants or a collection

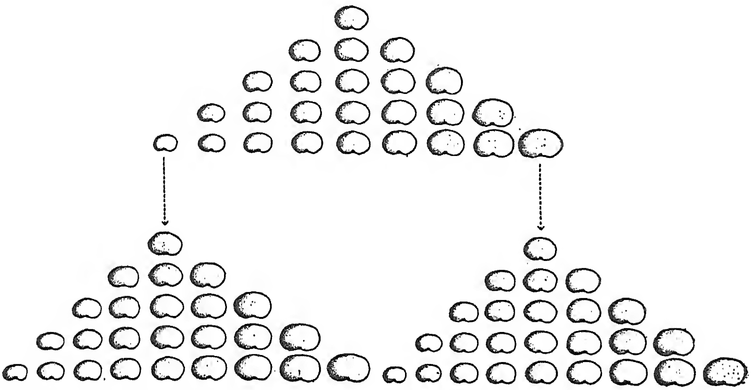


FIG. 127.—Diagram to show the inefficacy of selection when applied to a pure line. Above is the frequency distribution of the beans from one plant. Below are the distributions of the progenies grown from the largest and from the smallest beans. (*After Baur.*)

of bean seeds derived from different plants represents, according to Johannsen, a mechanical mixture of individuals differing in inherited factors for seed size. Selection in such cases, by seizing upon and isolating genetic differences, results in a resolution of a mixture of genotypes into true-breeding lines and is thus effective.

TABLE XVIII.—THE RESULTS OF SELECTING THE LARGEST AND THE SMALLEST SEEDS IN TWO LINES OF BEANS DESCENDED FROM A SINGLE PLANT (*Data from Johannsen*)

Generation	Average weight of selected parent seed		Average weight of progeny seeds	
	Lighter seeds	Heavier seeds	From lighter parent	From heavier parent
1	60	70	63	65
2	55	80	75	71
3	50	87	55	57
4	43	73	64	64
5	46	84	74	73
6	56	81	69	68

Johannsen distinguished two classes of variations: (1) genotypic variations, or differences in the genotype or hereditary constitution; (2) phenotypic variations, caused by the combined action of many non-heritable factors. Selection is effective only when applied to the first class.

Pure Line Defined.—Johannsen convincingly demonstrated that *selection among the progeny of a single genetically pure self-fertilized individual* was ineffective. He called such a group of descendants a *pure line*. At present the term is more broadly defined as a group of individuals all of which have the same homozygous genotype. Thus among self-fertilized plants, or among animals which reproduce by fission, parthenogenesis, or other methods not involving cross-fertilization, all the progeny of a single individual (provided no mutations occur) belong to the same pure line. Among cross-fertilized plants and the higher animals, where self-fertilization does not occur, individuals all of the same genotype may be expected after many generations of close inbreeding, although even continued mating of brother by sister does not in practice give the genetic identity which characterizes the individuals of a completely pure line. Lines pure in all of their traits are thus rare among most of our domesticated animals and cross-fertilized plants, but the pure line theory, nevertheless, applies to these cases as well as to self-fertilized plants, for its essence is that selection is ineffective on characters which are genetically pure or homozygous, and individuals homozygous for one or a few characters can be obtained even when complete homozygosity in all traits is not attainable.

Selection is relatively ineffective in changing the breed characteristics of a well-established variety, such as the white plumage, round body shape, and rose comb of Wyandotte fowls; but if such a uniform type is crossed, for example, with a pure-breeding game variety with colored plumage, long body shape, and pea comb, the F_2 generation consists of a complex mixture of heterozygous types. Selection practiced on such a group is immediately effective. Lines pure in recessive traits, such as single comb, or white plumage, can be isolated by a single selection, and the population can be rapidly broken up into a number of relatively pure lines within which selection again becomes ineffective.

The effectiveness of selection depends, therefore, on the presence of genetic variability. A practical demonstration of this has been given by Luther Burbank, whose ability to "create"

improved varieties of plants is well known. Burbank's success has depended on his skill in recognizing valuable variations occurring among large numbers of offspring from hybrid or heterozygous plants.

Fortunately for the breeder who wishes to change the character of his stock, the inherited factors affecting such valuable traits as milk production, weight, egg production, and crop yield are so numerous, and the domesticated animals and cross-fertilized plants so heterozygous or heterogeneous in respect to these factors, that selection practised on ordinary stock is often effective, and some advance is frequently obtainable. But after the initial period of selection is over, the stock approaches homozygosity and takes on some of the characteristics of pure lines, so that selection becomes less and less effective, and the breeder must seek some other means of improving his stock.

The pure-line theory has led to a general conception of the way in which selection accomplishes its results. According to this explanation selection merely sorts out and isolates the genetic factors responsible for the characters selected, and does not of itself create anything new.

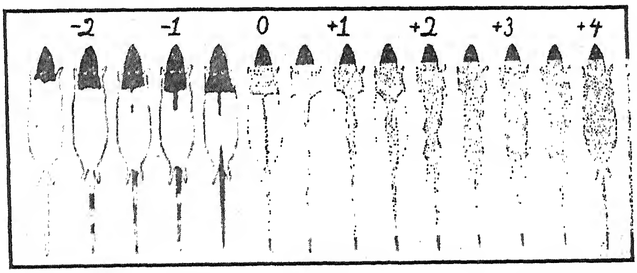


FIG. 128.—Variation in the hooded pattern of rats. By selecting the lightest and darkest offspring for twenty generations, the extreme types at −2 and +4 were obtained. (*From Castle.*)

An alternative explanation of the changes produced by selection is that it may change the genes themselves. There is no critical evidence, however, to show that the gene for a character which has been subjected to selection has itself undergone any alteration. In the selection experiments of Castle and Phillips which were effective in changing considerably the amount of white spotting in the hooded pattern of rats, the results are adequately explained by the hypothesis that selection has brought about the accumulation in the one line of modifying factors

tending to make the coat darker, and in the other line of factors tending to make the coat whiter (Fig. 128). Such modifying factors have been shown to be separable from the chief spotting factor. That selection accomplishes its results by isolating and accumulating factors rather than by altering the genes themselves is now generally accepted as most in accord with the experimental results.

Mass Selection.—The basic principle of selection is to choose for breeding those individuals which vary in the desired direction.

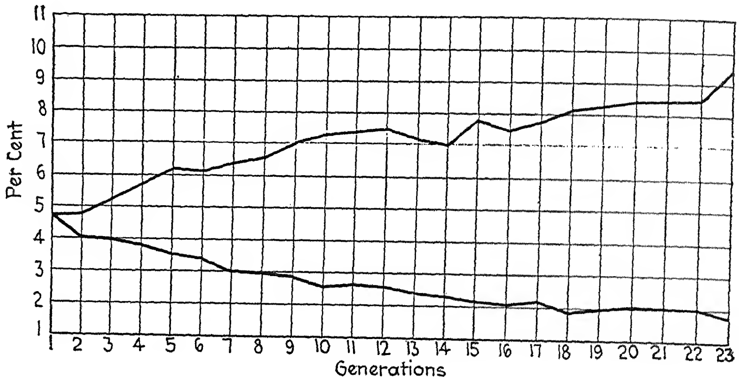


FIG. 129.—The results of selecting for high and for low protein content of corn at the Illinois Agricultural Experiment Station. (*After East and Jones.*)

The usual method is to judge the group of individuals by their visible or measurable characters and to rear all of the progeny so chosen. This is the method of the corn grower who at harvest time selects the best ears from the whole yield and rears his next year's crop from such seed. Such *mass selection* has been followed by plant and animal breeders for many years, and while slow and uncertain has led to the origin of improved varieties of both plants and animals.

An example of the efficacy of this method as applied to a cross-fertilized plant is shown in the results of a selection experiment with corn. In 1896 selections for high and low protein and high and low oil content of corn seeds were begun at the Illinois Agricultural Experiment Station. In each generation the seeds were chosen from the plants which showed on analysis the highest and the lowest percentages of protein and of oil. Each group was grown separately. The results of twenty-three generations of such selection have been analyzed by East and

Jones (Figs. 129 and 130). Mass selection has plainly been effective in altering the chemical composition of the seeds. Most of the changes occurred in the earlier generations and are probably due, as East and Jones believe, to the isolation of genotypes from the original mixed material with which the experiment began.

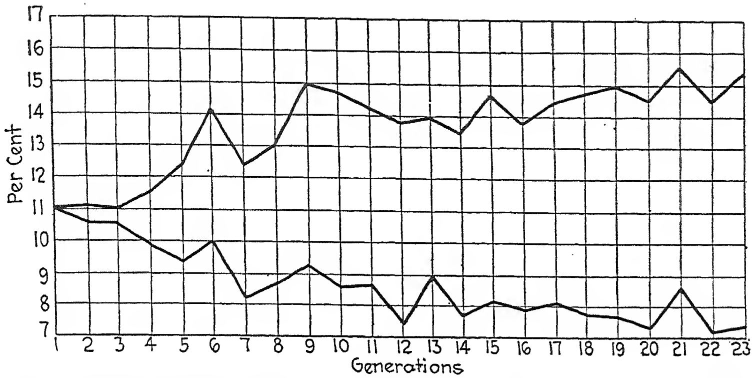


FIG. 130.—The results of selecting for high and low oil content of corn. (*After East and Jones.*)

Mass selection unaccompanied by inbreeding is not always effective, however. A selection experiment to increase the egg production of fowls was begun at the Maine Experiment Station in 1899. Only females which had laid at the rate of 160 eggs or more per year were used for breeding, while males were selected only from mothers which had laid 100 eggs or more. The highest producing individuals were mated at random. Selection on this basis for nine years failed to increase the average annual egg production of the flock, and it was abandoned in favor of a type of genotypic selection which will be discussed later. Other investigators, on the contrary, and many practical poultrymen, have succeeded in increasing egg production through the use of mass selection coupled with some knowledge of the genotypes of the individuals selected.

Mass selection is generally effective because most of the characters on which it is employed are apparently dependent on a large number of inherited factors, which may be slowly sorted out and accumulated by selection; but where such differences do not exist, or where for other reasons they cannot be sorted out by mass methods, mass selection is ineffective.

The same methods of selection may frequently be made to accomplish results more rapidly when some system of inbreeding is employed. Thus East and Jones have shown that the chemical composition of corn may be altered by selection within self-fertilized plants more rapidly than under random mating, such as that employed in the Illinois experiments. The same is true among animals bred by brother-sister matings, for the isolation of lines homozygous for the selected traits is much more rapid where relatives possessing the traits are mated.

The most rapid results accomplished by selection are those obtained in the sorting out of pure lines from a mixed population of self-fertilized plants, for here a single selection separates all of the genotypic differences at once. This accomplishes immediately all that is possible, for, as has been seen, selection within the pure lines is ineffective.

Progeny Selection.—It is certain, however, that *appearance*, the basis of choice used in mass selection, is alone not a reliable guide to breeding ability, for, some of the variations selected may be phenotypic rather than genotypic, and may thus not be inherited. A more certain method, which utilizes the modern knowledge of inheritance, is known as the *progeny test*. In adopting the progeny test, breeders have recognized that permanent improvement must be improvement of the genotype, and the problem is, therefore, to develop some method of estimating the genotype itself. The best evidence as to the genotypic constitution of an individual is obtained from a study of its progeny. Among plants, seeds from single individuals are planted separately and the progenies compared. The most uniformly satisfactory progenies are saved for further selection and the others are abandoned. Among animals the breeding value of a sire or dam may be best estimated from a sample of the early progeny. It is applied most readily to males, because of the greater number of offspring which may be obtained from a single male, and because flocks or herds may thus be improved with greater speed than through the selection of superior females. The males which produce the best progeny are retained; others, even though they are of desirable appearance themselves, are discarded. This method is probably not widely practiced in general animal breeding. Among cattle, for example, Pearl has found that most of the bulls used on farms are too young to have had daughters of known worth. With the system of

registry adopted by progressive breed associations it is now possible to estimate the relative values of a large number of sires from the performance records of their daughters. From a study of these records Gowen has found that although many much-used sires in the Jersey and Holstein breeds have improved the milk and the fat production of their daughters, others which have also sired a large number of daughters have caused no such improvement. The presence of the first class indicates either that the result of the progeny test confirms the value of other criteria used in selecting sires or that the sires were directly selected on the basis of their progeny tests. The presence of the second group, those sires which did not improve their daughters' production, may mean either (1) that these bulls were mated with females of such high production that further increase was not to be expected, or (2) that their genotype did not contain factors for the highest production, but that they were selected for breeding because of other excellencies, such as appearance and pedigree. In either case it is probable that the fullest use of the progeny test is not yet being made, and that selection based on this test may or may not agree with selection based on other criteria. The geneticist would recommend that, wherever possible, the basis of selection should be the progeny test, since this provides a more accurate indication of breeding value.

The method in its simplest form may be illustrated by a problem frequently encountered in poultry breeding. The standard requires that White Wyandotte fowls shall have rose combs; yet, in spite of having selected only rose-combed fowls for breeding for a number of generations, many breeders of this variety still find single-combed chicks among the progeny of their pure-bred birds. Ordinary selection has not eliminated the single combs. This may be done, however, and the stock made pure for rose comb, by progeny testing. Some rose-combed Wyandottes must apparently be heterozygous for single comb, since single comb is recessive to rose. If a number of rose-combed birds, male and female, are mated with one of the sporadic single-combed birds (or any single-combed bird), those which are pure for rose comb will produce only rose-combed chicks while the heterozygous individuals will produce equal numbers of rose and single comb offspring. Such heterozygous parents should then be discarded. Matings among the pure rose-combed males and females will never produce any singles, and the stock

should, in the absence of outcrossing or mutation, remain pure for rose comb.

Inheritance of Egg Production.—The same method has been used by Pearl, Goodale, and others in improving egg production in fowls. Pearl found that mass selection for higher egg production was ineffective. He then studied the inheritance of egg production in carefully planned experiments and proposed the following hypothesis:

The rate of fecundity or egg production depends on an interaction between a normally functioning reproductive system, a favorable environment, and at least two genetic factors for high production which may be called M and L. Both of these factors are dominant, and the former (M) is sex-linked while the latter (L) is not. A female with both of these factors (ZM)W LL or (ZM)W Ll is genotypically of high fecundity, laying thirty eggs or more in the four winter months, November 1 to March 1; a bird with either M or L alone, (ZM)W ll, (Zm)W LL, or (Zm) W Ll is genotypically of medium fecundity, with a winter production of from zero to thirty eggs. Birds with neither of these factors, (Zm)W ll are genotypically poor layers, producing no eggs in the winter. On this hypothesis, the chief problem in improving egg production is to find and breed from those fowls which have all of the factors for high production. If M is sex-linked, no females can be pure for this factor, since the female fowl is always heterozygous for sex-linked traits. But by progeny tests males can be discovered which possess one or both of these factors in homozygous condition. Since the factors are dominant, such males will transmit high egg production to their daughters. Males which contain neither of the factors may also be distinguished by progeny tests, and since these cannot transmit high egg production, they may be eliminated from the flock. An application of such progeny test selection resulted in doubling the average winter egg production of the flock in a period of six years. Goodale's studies failed to confirm Pearl's hypothesis that one of the fecundity factors was sex-linked, but showed that other factors in addition to those assumed by Pearl were involved. By progeny test selection based on his hypothesis Goodale achieved even more striking results, since the average annual egg production of his flock increased from 114 to 200 eggs in eight years. Whether or not one of the fecundity factors is sex-linked, selection based on the progeny testing of male fowls

is the most certain way of effecting genetic improvements in egg production.

The Breeder's Problem.—From the above discussion of selection, it can be seen that the breeder faces a threefold problem in bringing about permanent improvement in his plants or animals:

1. He must learn to distinguish environmental from genetic variations. Variations of the latter sort are the only kind which will yield to selection, whereas those of the former sort, such as the ones which occur in pure lines, are not amenable to selection.
2. He must know the genotype of the individuals with which he works and must recognize that breeding ability is more accurately gauged by the progeny test than by the appearance of the individual.
3. He must purify the desired genotype when it has been obtained, and produce lines which are pure or as pure as possible for a given set of characters. In animals and cross-fertilized plants this involves the adoption of some system of matings between relatives, or as it is more often called, inbreeding.

Systems of Mating.—All breeding operations which lead to the production of uniform and valuable varieties of animals and plants involve at some time the mating of relatives. To such matings the term *inbreeding* has been applied. Since, however, most animals and plants belonging to the same breed or variety are related in some degree, some inbreeding takes place whenever members of a breed or variety are mated. Inbreeding is thus a relative term covering a wide range of types of mating. In practice it has become convenient to restrict it to matings between close relatives, such as self-fertilization, brother by sister, parent by offspring, cousin matings, or others involving similar relationships. Matings between unrelated or distantly related individuals are said to constitute *outbreeding*, while the type of outbreeding which involves the mating of animals or plants belonging to different breeds or varieties is spoken of among breeders as *cross-breeding*. These two terms are often used interchangeably to denote matings between unrelated or distantly related individuals. Other terms are frequently employed especially among animal breeders, as, for example *line breeding*, which involves matings between relatives in an attempt to increase or concentrate in one line of descent the "blood" of one or a few individuals. These various systems of mating may all

be grouped under the two headings of inbreeding and outbreeding, which differ essentially only in the degree of relationship of the individuals mated.

The Results of Inbreeding.—Inbreeding has been consciously employed by animal breeders for two hundred years; it is the sole method of reproduction of many naturally self-fertilized plants, such as peas, beans, barley, and oats, and it has been increasingly used by plant breeders for the fixation of varieties of such naturally cross-fertilized species as corn. It has been occasionally practiced in the human race, as, for example, in the royal families of Egypt and to a lesser extent among the royal families of Europe. In spite of the evidence accumulated by such practical experience, there has been little unanimity of opinion with respect to the average results of inbreeding. Most breeders have found that this practice leads to increased uniformity, but some maintain that it results in decreased vigor and productiveness, while others have not come to this conclusion. Among plants, those which are regularly self-fertilized appear to be no less vigorous than those which are cross-fertilized, and the history of many of the best breeds of livestock shows that a considerable degree of inbreeding was involved in their production. On the other hand, it is very evident that continued close inbreeding had led to weakness in many animals, and to sterility, loss of yield, and other evidences of lack of vigor in plants.

This disagreement as to the facts involved has persisted among practical breeders. In human society it has resulted in laws and customs as diverse as those which forbid marriage outside of a restricted group of relatives and those which forbid matings between relatives altogether. Laws and breeding practices vary because inbreeding has not always produced the same results. Even though the facts vary, however, there has grown up among students of genetics a considerable degree of unanimity concerning the principles involved, and a general interpretation has now been proposed which explains the conflicting results in genetic terms. This change has been brought about through the accumulation of data from *controlled experiments* in inbreeding both animals and plants, and through the mendelian and biometric analysis of the evidence obtained.

The results of the early experiments on inbreeding small, rapidly reproducing animals (such as rats and mice) appeared to

verify the common conception that fertility and vigor declined, while disease, mortality, and abnormalities increased under inbreeding. The most extensive experiments on inbreeding in animals, however, have failed to verify entirely the earlier results. One of these later experiments, conducted by Miss King, has involved the inbreeding of the common rat for twenty-five generations, with a total production of about 25,000 young; while experiments on close inbreeding in guinea pigs have been carried on by the United States Department of Agriculture continuously since 1906, and when reported by Wright in 1922, had involved records on 30,000 animals and a maximum of twenty-three generations of close inbreeding. In both sets of experiments the closest possible inbreeding was employed. The chief characters measured were fecundity, weight, speed of growth, mortality, and other elements of vigor.

Experiments with Rats.—The experiments of Miss King began with a litter of four albino rats, two males and two females, from

FIG. 131.—Graph showing the average size of the litters produced by rats in successive generations of inbreeding. (*After King.*)

a uniform laboratory stock. These were inbred brother by sister. Little selection was practiced in the early generations, but after the sixth only the most vigorous animals were selected for breeding. The effects of inbreeding on the average size of litters produced are given as representative of the general results (Fig. 131).

In the first six generations, the inbred rats showed a decline in fertility and other elements of vigor. Non-inbred stock rats, however, showed similar changes at this time, and the food of all the animals was improved, with the result that both inbred and stock rats showed considerable improvement in fertility and growth after the sixth generation. After this time no decrease in vigor was noted in the inbred animals. On the contrary, their fertility appeared to increase somewhat during continued inbreeding with selection for vigor, and the growth and final size of one inbred series came to be definitely greater than was found in the non-inbred stock rats. This extensive and carefully conducted experiment at once showed that inbreeding accompanied by selection does not necessarily produce any adverse effects.

Experiments with Guinea Pigs.—The experiments on guinea pigs were begun with a larger series of less closely related individuals and were carried on by brother-by-sister matings within a number of different families. Comparisons between families and a study of the results of crossing members of different families could therefore be made, as well as a direct measurement of the general effect of inbreeding on various traits. According to Wright, the average effect of continued inbreeding on guinea pigs has been to produce a decline in all elements of vigor. The mortality at birth and between birth and weaning; weight; growth; size and number of litters, and resistance to tuberculosis have been adversely affected, and the inbred guinea pigs are, in general, inferior to the outbred controls in these respects. A result fully as important has been (to quote Wright):

> . . . the conspicuous differentiation among the families, which has been brought to light and increased by inbreeding. This has been most obvious in the fixation of such characteristics as color, number of toes, and tendency toward the production of particular types of abnormalities. There has also, however, been a significant differentiation in the averages made in all elements of vigor. These elements of vigor proved to be inherited independently of each other. Each family has come to be characterized by a particular combination of traits, usually involving strength in some respects with weakness in others.

The decline in vigor was an average result, but it took place in different ways in different families. "The fact that inbreeding of the closest possible kind has been carried on for over

twenty generations without obvious degeneration is a noteworthy result." (Wright.) The latter conclusion is in harmony with Miss King's and indicates that inbreeding of and by itself is not necessarily accompanied by degeneration. The results of inbreeding experiments with swine and with poultry agree in general with those obtained with guinea pigs. Hays' observations of the inbred litters produced by swine show that they were inferior to outbred litters in fertility, growth rate, weight, and mortality. During continued brother-sister matings in poultry, fecundity and growth rate have decreased, while the mortality rate for embryos, chicks, and adults has increased. Some differentiation in these traits has been noted among the inbred families. These results will be reconciled later with those obtained with rats.

Inbreeding Experiments with Plants.—The data obtained from inbreeding plants agree in general with the evidence from animals. The most extensive experiments have been those carried out on corn by Shull, East, Jones, and others. The corn plant is normally cross-fertilized. The wind carries the pollen from the tassels of one plant to the silks of another. It is a comparatively easy matter, however to fertilize the ears with pollen from the same plant. The inbreeding involved in such self-fertilization is much closer than is possible in animals, where two different individuals must be mated. Self-fertilization may thus be expected to produce the characteristic results of inbreeding in a smaller number of generations than can even the closest possible inbreeding in the higher animals.

Strains of corn have been carried on by self-fertilization for fifteen generations at the Connecticut Experiment Station, and from these and other strains inbred for shorter periods at Connecticut and other stations, there has been accumulated a greater amount of experimental evidence on inbreeding than exists for any other plant or animal. The following digest of this evidence is based on the recent summaries of East and Jones.

When the normally cross-pollinated corn plant is self-fertilized for a number of generations, the following results are obtained:

1. There is a progressive *decrease* in the *size* of the plant and in *yield* (Table XIX), which is most marked during the first few generations of inbreeding. After seven or eight generations the inbred lines tend to remain stable and to suffer little further decrease.

TABLE XIX.—THE EFFECT OF CONTINUED SELF-FERTILIZATION UPON THE YIELD AND HEIGHT OF FOUR LINES OF DENT CORN (*Data from Jones*)

Number of generations selfed	Yield per acre in bushels	Height in inches	Yield per acre in bushels	Height in inches	Yield per acre in bushels	Height in inches	Yield per acre in bushels	Height in inches
0	75	117	75	117	75	117	75	117
1– 5	64	87	51	81	58	91	41	77
6–10	45	97	38	85	39	88	34	82
11–15	38	97	34	84	30	87	28	82

2. Well-marked heritable differences in morphological characters appear among the inbred lines. The lines come to differ in such traits as color, shape, and size of seeds, cobs, and silks; arrangement of kernels on the ear; form of plant, and so on.

3. These differences tend to become constant or fixed in the lines, resulting in a progressive reduction in variability within each line. As the inbred line acquires a greater uniformity, it ceases to decline in growth and yield.

4. Many defective plants, such as albinos, dwarfs, and sterile individuals, appear in the course of inbreeding.

5. These effects of inbreeding operate for a limited number of generations, after which the inbred lines, although less vigorous than the original parents, are stable, healthy, and functionally normal.

The inbreeding of both plants and animals is thus found to have two principal effects: (1) a reduction in the variability of inherited characters within inbred lines or families, so that members of such families come to resemble each other more and more closely; (2) a usual (though not inevitable) decline in vigor.

Hybrid Vigor or Heterosis.—These two general results have given the clue to an explanation of the phenomena of inbreeding and outbreeding, but before this can be fully grasped, more data on the results of crossing distantly related individuals must be presented. It has long been recognized that crosses between different strains, varieties, or races of animals and plants frequently produce very vigorous progeny. The mule is a familiar example of the vigorous type that may result from the hybridization of two distinct species, while varietal and breed crosses are frequently employed in farm practice, such as the cross of Duroc-Jersey and Berkshire swine to produce a rapidly growing, early

maturing porker, or the cross of Aberdeen Angus by Shorthorn cattle for the production of large, well-formed beef cattle. Among plants the increased size, speed of growth, and earliness of maturity of specific and varietal crosses have been recognized for centuries. To such manifestations of vigor following out-breeding or crossing, the name *hybrid vigor* has been given, although this is now being superseded by the newer term *heterosis*, which is at once descriptive and explanatory. Such an increase in vigor following crossing is plainly the opposite of the decrease which frequently follows inbreeding (Fig. 132).

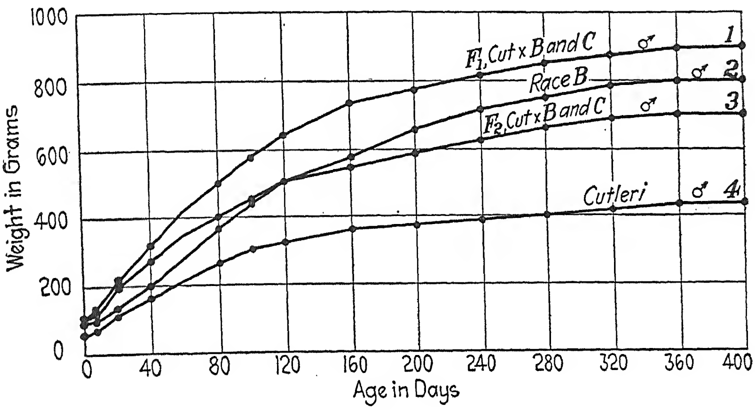


FIG. 132.—Hybrid vigor in guinea pigs. Growth curves of males of a large domesticated race of guinea pigs (race *B*, line 2); of a small wild race from Peru (*Cavia cutleri*, line 4); and of the F_1 (line 1) and F_2 (line 3) males from a cross of race *B* (and race *C* of similar size) with *Cavia cutleri*. The F_1 animals exceeded both parent races in growth rate and final size. The F_2 animals were distinctly smaller. (*After Castle.*)

This phenomenon, like inbreeding, has been observed and measured in recent experiments with animals and plants. Thus Wright observes in his analysis of the guinea pig experiments previously cited that "crosses between different inbred families have resulted in a marked improvement over both parental stocks in every respect." The increase of the F_1 outbred guinea pigs over their inbred parents amounted in the case of adult weight to twelve per cent, resistance to tuberculosis twenty per cent, rate of gain of young sixteen per cent, while mortality was reduced by eleven per cent. "The relatively small improvement in cross-bred matings in each separate respect is compounded into an advance of over eighty per cent in the combination."

Hybrid vigor, however, is most noticeable only in the first generation following the cross, and gradually disappears in later inbred generations. The long-continued experiments with maize provide the best illustration of this fact. If two inbred lines of corn each breeding true to the short stature characteristic of such lines are crossed, the F_1 plants are much taller than either parent type (Fig. 133), are more vigorous in all respects, and may yield more than twice as much grain as the parent strains. They are, moreover, just as uniform in all respects as the parent

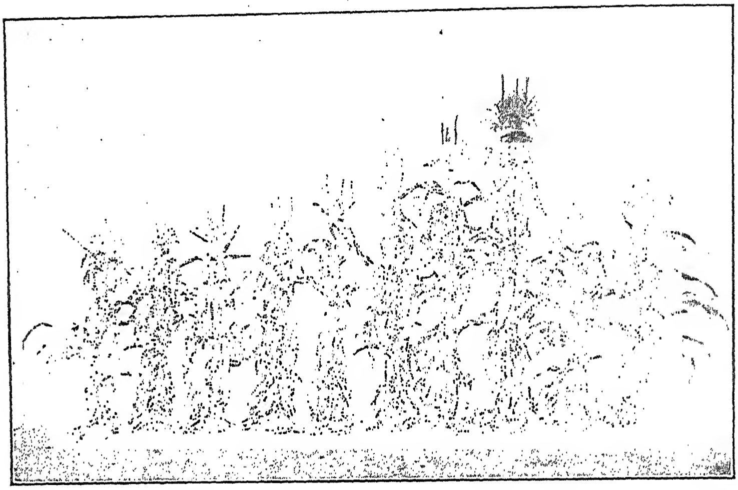


FIG. 133.—The effects of inbreeding after crossing. Representative corn plants of the two parent strains at right, followed by plants from the F_1, F_2, F_3, F_4, . . . F_8 generations of inbreeding toward the left. (*From Jones.*)

types. If these F_1 plants are self-fertilized, the usual effects of inbreeding again become evident. They decrease in size and yield, at first rapidly and later more slowly, until in the seventh or eighth generation the lines appear again to be stable and constant.

Genetic Interpretation.—The typical results both of inbreeding (decrease in size and vigor, decrease in variability) and of crossing (hybrid vigor, new combinations of traits) have now been interpreted in terms of mendelian inheritance. This interpretation is based on the effect of inbreeding and of crossing on the relative degree of homozygosity and heterozygosity which they tend to bring about.

The chief effect of inbreeding or the continued mating of close relatives is to *increase* the proportion of *homozygous* factor pairs and to *decrease heterozygosity.* If all plants of an F_1 population which is heterozygous in a single factor-pair (Aa) are artificially self-fertilized, the F_2 population consists, as Mendel showed, of one-fourth AA, one-half Aa, and one-fourth aa. Two of these classes are homozygous and will continue to breed true when self-fertilized, while the heterozygous class will again break up into one-fourth AA, one-half Aa, and one-fourth aa. If self-fertilization of all individuals is continued, the proportion of heterozygotes becomes steadily reduced by the breaking up of the Aa class into AA and aa types, and the proportion of homozygotes steadily increases, because these remain homozygous when formed and are augmented in each self-fertilized generation. This reduction in heterozygosity takes place automatically in all factor pairs regardless of the numbers involved, and the rate of reduction depends on the degree of inbreeding practised. Reduction is most rapid under self-fertilization, is less rapid under brother-sister matings, and does not take place at all under continued mating of second cousins. Theoretically it is found that practically complete homozygosity should be attained in the tenth generation of self-fertilization, at which time brother-sister matings starting with heterozygotes should have reduced the proportion of heterozygotes from 50 to about 5 per cent. This theoretical expectation is not likely to be realized in practice, because breeding is seldom at random as required by theory. Selection, both natural and artificial, is likely to preserve more heterozygous than homozygous individuals and, as explained below, many homozygotes are eliminated because of weakness or defects. It is, nevertheless, true that inbreeding tends progressively to increase homozygosity.

The effect of crossing, on the other hand, is very obviously to *decrease homozygosity* and to *increase* the proportion of *heterozygous* factor-pairs, by bringing together large numbers of contrasted factors.

Homozygosity (the result of inbreeding) seems thus to be related to decrease in vigor, and heterozygosity (the result of crossing) to be related to increase of vigor. This is the mendelian statement of the results of these two systems.

Now the important fact which seems to explain this connection between these factorial relations and vigor is that *recessive factors*

are more frequently harmful than beneficial to the organism. In a heterozygous population, recessive factors are hidden, but inbreeding results in their segregation in a homozygous condition and thus allows them to come into expression. Frequently these recessive variations are definitely lethal and prevent the normal development of the individual. Aside from such specific effects, however, it is known that all mutant factors have a general effect on other parts of the body, and this effect is seldom in the nature of an improvement in the balanced condition which has been brought about through the action of natural selection. Increased homozygosity is also likely to result in the loss through segregation of some of the factors on which maximum vigor depends. The decline in vigor when normally cross-bred animals or plants are inbred, and the increased uniformity within inbred lines are both functions of increasing homozygosity. The differentiation among inbred families which takes place under inbreeding may likewise be explained as due to the chance segregation of certain groups of factors into a given line and its subsequent fixation or purification through increasing homozygosity.

Diversity of Results Explained.—Some additional explanation is needed to interpret those cases in which vigor does not decline under inbreeding, as in normally self-fertilized plants or in the colony of rats which Miss King inbred for twenty-five generations. Here it must be supposed that the deleterious recessive factors to which the decline of vigor is ascribed are not present in any great abundance. Although harmful factors may be present in normal random-bred wild rats, it is probable that they had here been partially eliminated from the laboratory rats by some inbreeding before the experiment began, by chance choice of lines relatively free from them, and by selection during the course of the experiment. It is certain that not all strains of the same variety of animals or plants are alike with respect to such deleterious factors, for different lines and different varieties behave differently under inbreeding. Some families of guinea pigs declined rapidly under inbreeding and died out; others showed less loss of vigor. The same is true of inbred lines of corn, mice, and poultry. Some families of squashes, which are normally cross-pollinated, may be self-fertilized for many generations without deterioration while others cannot be. These differences in reaction are probably due to differences in genetic

constitution. If one makes a fortunate selection of one or a pair of parents which is relatively free from deleterious recessive factors, inbreeding may be pursued without its usual disadvantages. The relative freedom of such individuals from inherent weaknesses is due in some cases to chance, but usually to the amount of antecedent inbreeding. Thus individuals from normally closely bred stock, as a uniform colony of rats, are likely to be relatively homozygous, and further inbreeding produces no further change, while individuals from a normally crossbred stock or variety, for example corn or poultry, are likely to be heterozygous and to show considerable change under inbreeding.

These differences support rather than minimize the mendelian interpretation of the results of inbreeding. The results depend on the existence of many units affecting development, of which the recessive factors are likely to affect the organism adversely; on the distribution of these units in a population of a given character and history; and on the segregation and expression of these units as guided by a given system of mating. The evidence for this interpretation is convincing. It has led to the statement by East and Jones that inbreeding exerts its effects purely through the medium of inheritance, and not through the mere fact of blood relationship between the individuals mated.

Explanation of Heterosis.—The current explanation of heterosis or hybrid vigor rests on precisely the same assumption and reasoning. Inbred lines or pure varieties of animals and plants contain different factors affecting rate of growth, fertility, and size. They have become different through segregation, isolation, and fixation of different factors by inbreeding. It has already been noted that recessive factors are more frequently deleterious, and that factors making for vigor more frequently show dominance. It is only necessary to add the assumption that the effects of such dominant factors are *cumulative*, in order to see why the F_1 offspring from a cross of individuals from different inbred families may be larger and more fertile, and may grow more rapidly than their parents. Assume, for example, that the growth of the plant in one inbred line of corn is in part controlled by four factors, A, B, C, D, each of which tends to increase the vigor and growth of the plant, and that each is dominant or partially dominant to its allelomorph which has a lesser effect on growth. The same degree of growth in another inbred line is

effected through four factors E, F, G, H, each tending to increase growth and each at least partially dominant. If two such plants are crossed, the hybrid will have the composition $ABCDEFGH$, and will thus contain eight different dominant factors, each of which has the effect of increasing the growth of the plant. Such a hybrid should attain a greater growth than either parent which had but four growth factors. This is an extreme case, and the assumptions of dominance and equal effect of different factors are not entirely justified by experimental results, but that some cumulative combinations of this sort take place when inbred lines are crossed can scarcely be doubted in the face of the frequency with which the phenomenon of hybrid vigor takes place, and particularly in view of the experiments with corn and with guinea pigs in which the results have been most carefully observed. Thus Wright is able to conclude from a study of inbreeding and cross-breeding in guinea pigs:

> Analysis of the various crosses indicates that the results are all the direct or indirect consequence of the mendelian mechanism of heredity. The fundamental effect of inbreeding is the automatic increase in homozygosis in all respects. An average decline in vigor is the consequence of the observed fact that recessive factors, more extensively brought into expression by an increase in homozygosis, are more likely to be deleterious than their dominant allelomorphs. The differentiation among the families is due to the chance fixation of different combinations of the factors present in the original heterozygous stock. Crossing results in improvement because each family in general supplies some dominant factors lacking in the others. Dominance or even imperfect dominance in each unit character is built up into a pronounced improvement over both parent stocks in the complex characters actually observed.

The increased vigor of first generation cross-breds may thus be accounted for on the assumption that unlike factors for vigor are combined in this generation. Both the experience of the practical breeder and the results of experiment show that this added vigor is not permanent but declines under renewed inbreeding after the first generation. This must necessarily be the case, on the assumption made, since inbreeding increases homozygosis and vigor depends on heterozygosis (heterosis). Jones has suggested that the maximum number of different factors (on which maximum vigor apparently depends) can be accumulated only in the first generation, since linkages between the numerous factors involved (which are probably distributed

through all the chromosomes) will make it improbable that the maximum number of combinations can be obtained in any later inbred generation.

The conclusion follows that the results of inbreeding and of out- or cross-breeding are the necessary consequences of the same mechanism of heredity which has already been found to govern the inheritance of simple alternative traits.

The Measurement of Inbreeding.—Since inbreeding is a relative term, some method of measuring the degree of inbreeding involved in different systems of mating is needed. To meet this requirement Pearl has proposed a *coefficient of inbreeding* which can be applied where pedigrees for several generations are known. This coefficient is based on the fact that inbred individuals have fewer than the maximum possible number of different ancestors. Thus an animal or plant descended from matings between unrelated ancestors has two parents, four grandparents, eight great-grandparents, and so on; but an individual whose parents were cousins has only six different great-grandparents, since two of his grandparents were brother and sister. Similarly, an animal descended from brother-sister matings has only two different grandparents instead of four. Such a coefficient for a given generation may be obtained by counting the number of actually different ancestors in that generation of a pedigree, subtracting this from the maximum possible number of different ancestors *in that generation* and dividing the difference by this maximum possible number of ancestors. The result may be stated as a percentage of the maximum number, and derived by the following formula:

$$\text{Coefficient of inbreeding} = 100 \times \frac{\text{Difference between the maximum possible number of ancestors and the actual number of ancestors, for a given generation}}{\text{Maximum possible number of ancestors for that generation}}$$

The coefficient of inbreeding for a given individual is, therefore, merely that percentage of the maximum possible number of ancestors in a given generation which consists of individuals appearing more than once in that generation (or some preceding one). Thus if an animal is descended from brother-sister matings, both its parents must be different, and for this generation his coefficient of inbreeding is $0\left(\frac{2-2}{2}\right)$; but of his grandparents

- Roan Gauntlet
  - Royal Duke of Gloster
    - Grand Duke of Gloster
      - ×Champion of England
        - ×Lancaster Comet
          - ×Queen's Roan
          - ×..............
        - ×Virtue
          - ×Plantagnet
          - ×Verdant
      - Duchess of Gloster 9th
        - Lord Raglan
          - Crusade
          - Brenda
        - Duchess of Gloster 6th
          - Lord Carlies
          - Duchess of Gloster
    - Mimulus
      - ×Champion of England
        - ×Lancaster Comet
          - ×Queen's Roan
          - ×..............
        - ×Virtue
          - ×Plantagenet
          - ×Verdant
      - Mistletoe
        - ×Lord Raglan
          - ×Crusade
          - ×Brenda
        - Maidstone
          - Matadore
          - Phantassie
  - Princess Royal
    - Champion of England
      - Lancaster Comet
        - Queen's Roan
          - Will Honeycomb
          - ....
        - ....
          - ×Will Honeycomb
          - Lupin
      - Virtue
        - Plantagenet
          - Duke of Lancaster
          - Madaline
        - Verdant
          - Exchequer
          - Prigg
    - Carmine
      - Czar
        - ×Lord Raglan
          - ×Crusade
          - ×Brenda
        - Corianda
          - Baron
          - Czarina
      - Cressida
        - John Bull
          - Rumous
          - Mayoress
        - Clipper
          - Billy
          - ....

Coefficient of inbreeding, $Z_n = \frac{100(p - q)}{p}$.

p = possible number of ancestors
q = actual number of different ancestors
n = 1 = parental generation; 2, grandparental, and so on
or this animal, therefore,

$$Z_1 = \frac{100(p - q)}{p} = \frac{100(2 - 2)}{2} = 0.$$

$$Z_2 = \frac{100(4 - 4)}{4} = 0.$$

$$Z_3 = \frac{100(8 - 6)}{8} = 25 \text{ per cent.}$$

$$Z_4 = \frac{100(16 - 10)}{16} = 37.5 \text{ per cent.}$$

$$Z_5 = \frac{100(32 - 19)}{32} = 40.6 \text{ per cent.}$$

FIG. 134.—Method of calculating the coefficient of inbreeding from a pedigree. Each name that appears more than once in a given generation, or which has appeared earlier in the pedigree, is crossed off. When an individual is once crossed off, all of its ancestors can be crossed off as far back as the pedigree goes.

50 per cent $\left(\frac{4-2}{4}\right)$ are duplicates or appear more than once in the pedigree, and 75 per cent $\left(\frac{8-2}{8}\right)$ of his great-grandparents do so. His coefficient for these past two generations is thus 50 and 75 per cent, respectively. The use of this formula (reduced to algebraic terms) in determining the coefficient of inbreeding of the Shorthorn bull, Roan Gauntlet, is illustrated in Fig. 134.

It is frequently necessary to consider the relationship involved between the father's and mother's side of the pedigree, since in a cross between individuals descended from two different inbred lines the coefficient of inbreeding may be high, although the animal itself is not inbred but cross-bred. The *coefficient of relationship*, K, is simply the per cent of individuals in the father's and mother's sides of the pedigree which appear on both sides.

These two coefficients state in concise form what is known about the inbreeding and relationships involved in the pedigree of any individual. They are useful in determining how near the inbreeding involved in a particular case approaches that resulting from a formal system of matings such as that of brother by sister. In the illustration used, the coefficient of inbreeding in the fourth ancestral generation of Roan Gauntlet is 37.5 per cent, while in an animal descended by brother-sister matings the coefficient in this generation has a value of 87.5 per cent. Roan Gauntlet is, then, less than half as inbred as he would have been if his ancestors for four generations had been brothers and sisters. Although inbred animals are, in general, more homozygous than outbred ones, a high coefficient does not indicate that the animal concerned is homozygous. It only makes the *probability* of his being relatively homozygous greater than in the case of an animal chosen at random from a less inbred population.

Breeders' Beliefs.—While the results of controlled experiments have in general confirmed the experience of practical breeders with respect to selection and inbreeding, they have failed to corroborate a number of other conclusions frequently drawn by breeders. Such beliefs as the existence of "telegony," "saturation," "infection," and "maternal impressions" have been definitely reduced to the status of myths unsupported by critical evidence, while other conclusions derived from such actual occurrences as reversion, atavism, and prepotency have

been shown to rest not on mysterious causes but on the normal mechanism of heredity.

The belief in "telegony," or the influence of a previous mating on later offspring, probably arose from instances of pure coincidence of variation in the offspring of a single female. An outstanding case of telegony was the production of two foals showing traces of zebra-like striping by matings of a pure-bred black Arab stallion to a chestnut Arab mare which had previously produced one striped foal sired by a quagga, a zebra-like member of the horse family. Later experiments by Cossar Ewart with horse and zebra crosses showed that pure-bred matings occasionally produced striped foals and that previous mating of mares with zebras had no influence whatever on the occurrence of these or other zebra traits in later offspring.

"Saturation" is the alleged cumulative effect of telegony, whereby the successive offspring of the same mating bear increasing resemblance to the sire. All the available statistical evidence, however, indicates that this is not at all true and that there is no reason to doubt the correctness of the mendelian view that the hereditary qualities of successive offspring are determined by the random distribution of the factors at each maturation division.

"Infection" is the supposed ability of a male to transfer qualities from one female, with which he has been mated, to his later mates, or the tendency of a female to come to resemble a male with which she is repeatedly mated. In regard to hereditary characters, this belief is entirely illusory, though there can be no question that diseases such as syphilis may be transmitted in this way.

Among all classes of persons who are unacquainted with the biology of reproduction the belief persists that many peculiarities of the offspring are traceable directly to impressions received by the pregnant mother. Birth marks, slight defects, peculiarities of temperament, and other noticeable and unexplained traits have been ascribed to such "prenatal influences." There is not the slightest evidence, however, that there is any specific relation between the stimuli received by the mother and the peculiarities of the child. The condition of the mother during pregnancy is of great importance to the offspring, but it operates chiefly in providing adequate or inadequate nutrition to the developing embryo.

Prepotency.—With respect to such beliefs as prepotency (the ability of a particular parent, usually the sire, to impress its qualities on the offspring) and reversion or atavism (the resemblance of offspring to near or remote ancestors), the case is somewhat different, for these beliefs are founded on actual facts. Prepotency is usually an expression of the presence of homozygous, dominant factors in the genetic constitution of the prepotent parent. It relates not to general qualities such as strength, vigor, and masculinity, which are composed of many separate traits, but to specific qualities governed by inherited factors. Thus a male may be prepotent in respect to color and horn characters, since dominant factors for these traits may have become fixed and homozygous in him by inbreeding, but at the same time may not be prepotent in other characters, such as conformation and milk production, for which he may be heterozygous. Closely inbred individuals are more likely to be prepotent for several traits than random bred ones, because of the greater likelihood that the factors of the inbred individual have become homozygous. For this reason purebred sires, which are frequently somewhat inbred, often transmit valuable traits to their offspring by scrub or random-bred mates. The argument for "grading-up" by the use of purebred sires is strengthened by this fact.

Reversion, or the appearance of offspring resembling remote ancestors or the wild type, has for many years puzzled breeders. Actually it has a simple mendelian explanation. In the evolution of domesticated animals and plants the several factors on which a given trait depends may become separated into different individuals or lines, and the trait may disappear. Thus albino guinea pigs have apparently lost a factor which determines the development of full color, although most of them retain, unexpressed, the factor for agouti coat color of the wild ancestor. Black animals, on the other hand, seem to have lost the agouti factor which in combination with others produces the yellow- and black-banded fur of the wild type. When black is crossed with albino, one parent supplies the factor for color; the other, the factor for agouti; the genotype of the wild form (as regards coat color) is reconstituted, and agouti offspring result, which resemble neither parent but reproduce the color of the original or wild type. Many cases of this phenomenon have been investigated and found to have the same explanation (Fig. 37, page 96). *Ata-*

vism or resemblance of progeny to less remote ancestors is, like reversion, probably due to the recombination of mendelian factors.

The Prospects for the Future of Animal and Plant Breeding.—In what way can the recent developments in genetics be expected to aid in the improvement of the existing varieties of domesticated animals and plants? Some of the principles and methods on which genetics rests have already been used in breeding practice. That inheritance is a matter of individual traits and that the individual animal or plant must be the unit of all intensive breeding work is now recognized by progressive breeders. This has led to the introduction of the pedigree method, not only in the breeding of the larger farm animals but in plant breeding as well. Selection, based on individual worth, has already become common, and elaborate methods for measuring individual performance have come into use, such as milk measurement and testing, trap-nesting, classification and measurement of wool and meat, and the measurement of yield, disease resistance, and adaptability of individual plants and varieties. These developments will undoubtedly be continued and extended.

Progeny Testing.—In animal breeding, the facts of inheritance and the practical gains warrant a much greater use of the pedigree method, and of selection based on progeny test, rather than on individual performance only. In plant breeding the progeny test is being widely applied to naturally self-fertilized plants, such as the cereals, cotton, tobacco, peas, and beans. The basis of selection is the progeny of the individual plant rather than of the individual fruit or seed, since all plant structures have normally the same genetic constitution. Among cross-fertilized plants, such as corn, alfalfa, and beets, controlled pollinations, the production of pure lines by self-fertilization, and subsequent progeny testing have yielded valuable experimental results and must be employed to obtain new advances. One of the greatest gains to be expected from these methods of testing individuals is the increasing accuracy with which the truly inherited variations may be separated from those which are due to environmental factors. Many superior individuals when individually tested are found to owe their superiority to a fortunate temporary combination of circumstances rather than to a superior heredity. The progeny test in both animals and plants is the only certain method for avoiding the selection of such individuals and for aiding in the choice of inherently superior ones.

Indirect Selection; Judging.—A prerequisite to selection of any sort has been the ability of the breeder accurately to appraise the worth of an animal or plant by the closeness with which its individual traits approach an ideal or standard of value. Formal methods of judging have thence come into practice. If judging is to fulfil its true function of an aid toward improvement, the criteria used must have an intimate relation to fundamental traits which determine the economic value of the individual. Wherever this is the case, the breeder is able to practice an indirect selection on traits which are not immediately visible, such as milk production or yield, by means of traits which are readily visible, such as size, shape, proportions, or special marks. The labor of correlating these criteria with the deeper-lying traits has only just begun. For dairy cattle and corn, statistical treatment has shown that some of the criteria are useful in indicating economic value, while others are worthless. In the future this method will be more widely applied, and the standard requirements with regard to morphological traits will be re-examined in the light of their correlation with traits of economic importance.

New Applications of Selection.—Advances in other sciences have already added new tools to be used in selection. One of the chief problems confronting both the animal and plant breeder is the reduction or elimination of the diseases which at present exact such a heavy toll. One method through which relief has been sought is the breeding of disease-resistant strains. Increase in the knowledge of the causes and methods of transmission of diseases has made available methods of testing for susceptibility and resistance, and these may become the basis of selective breeding operations. Hybridization between resistant and susceptible varieties has proved the importance of heredity with respect to some specific diseases (wheat rust, corn smut, and tuberculosis) so that the prospects for advances in this direction are good.

Finally selection, however practised, is coming to have the object, not so much of perfecting a standard type, as of bringing about a combination of inherited characters which is adapted to a particular environment. The development of an individual or variety is determined by an intimate interaction between its inherited constitution and the conditions under which it lives, and its ultimate value depends on its adjustment to

these conditions. Some effort has been expended on breeding varieties of plants for particular localities, and the extension of this effort in both plants and animals will involve the use of all of the methods of improvement suggested above.

Inbreeding and Cross-breeding.—A new field for animal and plant improvement has been opened up by the newer knowledge

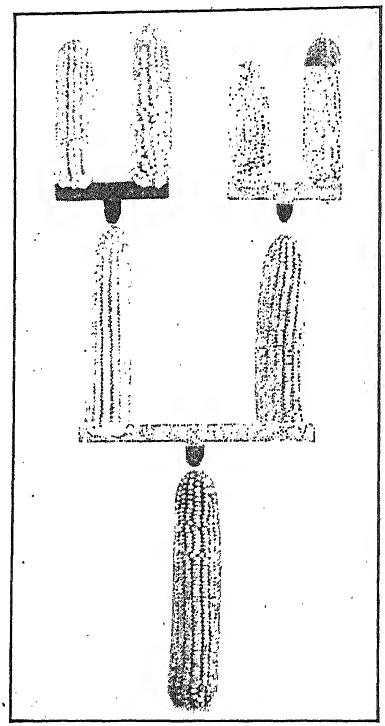


FIG. 135.—The effect of double-crossing on the yield of corn. At top, ears from four inbred stains, A, B, C, and D; second row, F_1 ears from cross of $A \times B$ and $C \times D$; at bottom, ear from cross of $AB \times CD$. (*From Jones.*)

of inbreeding and crossing. The application of these methods of mating has already resulted in definite improvements. Thus Jones has utilized the phenomenon of hybrid vigor to the fullest degree in improving the yield of corn. The great increase in vigor and yield which characterized the F_1 plants from a cross of two inbred strains has already been mentioned. If now four instead of two inbred strains are combined, the yield may be still

further increased. Jones has carried out such tests in the following way. Four lines *A*, *B*, *C*, *D* are selected from among strains which have been inbred for several generations. *A* is crossed with *B*, and *C* is crossed with *D* to produce two F_1 progenies. *AB* is then crossed with *CD*. Such "double-crossed" progeny have been shown by test to return a considerable increase in yield over any of the parent types and over selected corn grown by the ordinary methods (Fig. 135).

Wright suggests an important application of inbreeding in the improvement of livestock. Reasoning from the results of experiment with guinea pigs he says:

> Nearly all the characteristics dealt with here, like most of those of economic importance with livestock, are of a kind which is determined only to a slight extent by heredity in the individual. About 70 per cent of the individual variation in resistance to tuberculosis, and over 90 per cent of that in the rate of gain and size of litter is determined by external conditions. Progress by ordinary selection of individuals would thus be very slow or nil. A single unfortunate selection of a sire, good as an individual, but inferior in heredity, is likely at any time to undo all past progress. On the other hand, by starting a large number of inbred lines, important hereditary differences in these respects are brought clearly to light and fixed. Crosses among these lines ought to give a full recovery of whatever vigor has been lost in inbreeding, and particular crosses may safely be expected to show a combination of desired characters distinctly superior to the original stock. Thus a cross-bred stock can be developed which can be maintained at a higher level than the original, a level which could not have been reached by selection alone. Further improvement is to be sought in a repetition of the process, the isolation of new inbred strains from the improved cross-bred stock, followed ultimately by crossing and selection of the best crosses for the foundation of the new stock.

The ultimate practical problem in plant and animal breeding, as was suggested at the beginning of this chapter, is the control of inheritance. This control presupposes the power not only to manipulate inheritance by breeding operations, but also the power consciously to induce new heritable variations. This goal is probably a distant one, but the first steps toward it have been made, and greater progress may be expected in the future.

QUESTIONS FOR THOUGHT AND DISCUSSION

140. Why is the appearance and the behavior of an animal or plan not always a certain indication of the way in which it will breed?

141. What advantages does the animal breeder have over the plant breeder, and *vice versa?*

142. Animal breeding has progressed to a relatively higher state of development than plant breeding. Explain.

143. What advantages and what disadvantages has the breeder of plants like potatoes and fruit trees, which are normally propagated by vegetative means?

144. In livestock breeding much more emphasis is laid on the possession of a superior male than of superior females. Why?

145. Domesticated varieties of animals and plants are much more variable than wild species. Explain.

146. Why is less known about the genetics of domestic animals than about such species as mice, guinea pigs, and fruit flies, although the former are economically much more important than the latter?

147. Mendelian factors are definite units which, theoretically, may be shuffled and combined at will by the breeder. What obstacles are there in practice to making certain desired combinations of traits?

148. Explain the appearance of inferior animals ("purebred scrubs") in strains of purebred animals the great majority of which are superior individuals.

149. Do you think that the notable improvement during the past few decades in the individual production of milk, meat, eggs, and so on is due entirely to the development, by breeders, of progressively superior types of animals? Explain.

150. Aside from the practice of scientific breeding methods on the present domestic animals and cultivated plants, what other method can you think of for the production of new and superior types among them?

151. It is much more important to develop races of cultivated plants adapted to local conditions than it is to develop similar local races of domestic animals. Explain.

152. Why is disease resistance a much more important economic trait than it used to be?

153. Breeding and selection may render a race of plants apparently resistant to a given species of parasite, but if the plant is grown in a different region this resistance is sometimes found to be lacking even though the physical environment is exactly the same. Explain.

154. The chestnut bark fungus, introduced some years ago into the United States, has exterminated all the native American chestnut trees over a wide area. In China, its native home, the species of chestnut are almost immune to its attack. How do you explain this difference between American and Chinese chestnut trees?

155. An attempt was made to produce a *Phylloxera*-resistant variety of grape by crossing the European wine grape with resistant American stocks. No good, resistant wine grapes have been produced by this method. A valuable rust-resistant strain of wheat, however, was developed by crossing a good wheat type, susceptible to rust, with a rust-resistant type, and by subsequent selection among the offspring. Why do you think the attempt failed in the case of grapes and succeeded in the case of wheat?

156. How do you explain the fact that a union between two given parents is sometimes sterile when each of these parents is fertile if mated to another individual?

157. A breeder has a race of plants which has been self-fertilized for ten generations. He has repeatedly tried to increase the flower size of this race by selection, but to no avail. Explain why this is so. Finally, he crosses this race with another which is exactly similar to it in flower size. The hybrids resemble their parents, but by selection among the offspring of the hybrids the breeder is able in a few generations to increase the flower size considerably. Explain why this is so.

158. A breeder has a strain of small poultry and wishes to increase its size. He buys two cocks, equal in weight and both much bigger than his own strain. He breeds these with his own females, keeping the offspring of each cock separate, but continually breeding these offspring together and with the large cocks, carefully selecting for increased size all the while. He is able in this way to obtain birds among the descendents of cock A which are as big as A, but none bigger. Among the offspring of cock B, however, he is able to develop a strain considerably bigger even than B. Explain how this is possible on the basis of the multiple factor hypothesis of size inheritance.

159. In what sense is it true that selection has produced new types of animals and plants, and in what sense is it not true?

160. Selection is usually more effective with cross-fertilized than with self-fertilized plants. Explain.

161. Even within a pure line, it is often desirable to continue the practice of selecting superior individuals for breeding. Why should this be necessary if selection is ineffective in pure lines?

162. Will selection for dominant characters be more or less effective than for recessive ones? Why?

163. To what selective process other than that directed by breeders have domestic animals and plants been subjected?

164. No wild ancestors of corn are known and this species probably arose as a hybrid. What connection may there be between this and the fact that corn is one of the most adaptable of crop plants and that

among its large number of varieties there are some which thrive in the tropics and others in the north, and that others are adapted to all sorts of special conditions?

165. Since mass selection is so inferior to progeny testing as a means of establishing superior lines, how does it happen that mass selection is still so widely practiced?

166. Sometimes, particularly in the breeding of small grains, after a cross has been made to bring together a new combination of desirable traits, the F_2 and a few succeeding generations are planted broadcast and the seed all harvested together, before the breeder begins to practice the selection of individual plants. Explain the advantage of this method.

167. If a potato breeder desires to obtain a new variety of potatoes, would you advise him to plant "seed" potatoes (pieces of tuber) or real seed from the seed capsule, to provide plants among which he may practice selection? Why?

168. If selection in one sex proves to be more successful in improving a stock of animals than does selection in the other sex, what conclusion can you draw as to the method of inheritance of the character in question?

169. Many breeds of livestock, such as Jersey and Guernsey cattle, Berkshire swine, Shropshire and Dorset sheep, and very many others, did not originate through a conscious effort toward a definite type by breeders over a wide region but arose each in a very restricted area, each island or county often having its particular type. How do you explain this fact?

170. The inbreeding of normally cross-fertilized animals and plants is usually followed by a reduction in vigor. How is it, then, that many species of plants in nature are almost always self-fertilized and thus closely inbred, but still continue to thrive and maintain themselves successfully?

171. Will inbreeding result in the reduction of a heterozygous to a homozygous condition more rapidly in a species with a large number of chromosomes or in one with a smaller number? Explain.

172. If heterozygous individuals are more vigorous than homozygous ones, why is so much emphasis laid by animal breeders on the desirability of purebred animals which are relatively much more homozygous than ordinary stock?

173. What explanation have you for the fact that recessive traits are more often harmful than beneficial?

174. If a normally cross-fertilized animal or plant is inbred and its offspring, although suffering considerable loss of vigor, are able to survive, a strain produced by crossing these inbred types will usually be

more vigorous than the parent race from which the stock originated. Explain.

175. In what way is the phenomenon of heterosis of more economic value in the case of plants propagated vegetatively than in those which reproduce by seed?

176. In the method used by Jones for combining four inbred lines of corn (page 368), what will be the comparative vigor of the offspring of lines $A \times B$; lines $C \times D$; and of $AB \times CD$; and what will be the comparative *variability* of the offspring of these three crosses?

177. Why is selection for vigor in inbred lines likely to delay the attainment of complete homozygosity?

178. If two individuals of the same breed have the same coefficient of inbreeding, does this mean that they are similar genotypically? Explain.

179. How do you account for the widespread belief in "prenatal influences"?

PROBLEMS

243. A breeder has a group of animals all of which are heterozygous for a given dominant character A, and thus have the genotype Aa. He wants to establish a race homozygous for A. To accomplish this he allows these animals to interbreed freely, and then practices mass selection among their offspring, saving for breeding all individuals which show the character A and discarding only the aa animals. Members of one generation do not cross with any other. In the fifth generation, what proportion of the animals which have the character A will be homozygous for it? How could the breeder have established a homozygous strain more easily?

244. If the breeder mentioned in the previous question is practicing mass selection for *two* characters, A and B, and his original animals have the genotype $Aa\ Bb$, would selection be effective more rapidly or more slowly than when only one character was concerned? Explain.

245. Assume that you have a race of plants with the genotype $AA\ bb\ CC$ and another with the genotype $aa\ BB\ cc$, and that you wish to develop a race with the genotype $AA\ BB\ CC$. How would you go about it and how many plants would you have to raise?

246. A breeder has a homozygous race with three dominant factors, A, B, and C, and three recessive ones, d, e, and f, and another race homozygous for a, b, c, D, E, and F. He wishes a race homozygous for A, B, C, D, E, and F. If he crosses his two races, the F_1 will, of course, show all six characters but it will not breed true for them. What proportion of the F_2 raised from this cross will be the homozygous type which he desires? How may he discover which these individuals are? If you were confronted with this problem but were unable to raise the

very large number of individuals required to produce and discover the desired type in the F_2, but had more time to raise a larger number of generations, how would you proceed?

247. A certain corn plant produces, when self-fertilized, about 25 per cent of albino seedlings. What proportion of the green progeny plants would be expected to be free from this recessive lethal factor? How would you identify these plants and produce from them a strain free from this lethal defect?

248. A certain corn plant produces, when selfed, about seven-sixteenths of white seedlings which die (see Problem 122, Chap. V). Are the chances of obtaining from this plant a strain free from lethal defects better or poorer than in the preceding question? Why?

249. Peas are naturally self-fertilized. A breeder is endeavoring to develop a race of peas with very large seed and another with very small seed. He has a commercial variety of peas with seed varying from 0.50 to 1.50 grams, with a mean at about 1.00 grams. He selects for light seed, and plants *A* (0.52 grams), *B* (0.55 grams), *C* (0.54 grams), *D* (0.51 grams), and *E* (0.53 grams); and, for heavy seed, plants *F* (1.40 grams), *G* (1.39 grams), *H* (1.45 grams), *I* (1.47 grams), and *J* (1.39 grams). He raises the offspring of each of these separately. The mean weight of the seed of the offspring of *A* is 0.56 grams; of *B*, 0.94; of *C*, 0.58; of *D*, 0.52; of *E*, 0.59; of *F*, 1.38; of *G*, 1.00; of *H*, 1.49; of *I*, 1.40; of *J*, 1.44 grams. What conclusions can you draw from these results as to the composition of this commercial strain of peas; as to the practicability of further selection; and as to the best procedure for the breeder to follow in order to produce peas with distinctly larger and distinctly smaller seeds than he now has?

Note.—In the three following problems assume that egg production in fowls is inherited according to Pearl's hypothesis (page 348).

250. A breeder has two high-producing hens and five males, of unknown genotypes. Each hen is bred to each male, with results as follows:

Hen 1 × male 1 gives three-eighths high, one-half medium, and one-eighth low layers.

Hen 1 × male 2 gives one-fourth high, one-half medium, and one-fourth low.

Hen 1 × male 3 gives one-half high, one-half medium.

Hen 1 × male 4 gives three-fourths medium, one-fourth low.

Hen 1 × male 5 gives one-half medium, one-half low.

Hen 2 × male 1 gives one-half high, one-half medium.

Hen 2 × male 2 gives one-half high, one-half medium.

Hen 2 × male 3 gives one-half high, one-half medium.

Hen 2 × male 4 gives all medium.

Hen 2 × male 5 gives all medium.

What are the probable genotypes for fecundity of these seven birds? From which of these ten crosses would you be most likely to get the best males for producing high-laying hens?

251. Three males, A, B, and C, and two hens, D, and E, are all offspring of the same high-producing hen by the same male. Both daughters are high producers. Brothers are mated to sisters, with the following results:

$A \times D$ gives all high-producing pullets.
$A \times E$ gives three-fourths high, one-fourth medium.
$B \times D$ gives one-half high, one-half medium.
$B \times E$ gives one-fourth high, one-half medium, one-fourth low.
$C \times D$ gives all high producers.
$C \times E$ gives one-half high, one-half medium.

What are the genotypes of these five birds? of their parents? From which of these six matings would you save the males for breeding? From which would you save the females? Explain.

252. Calculate the coefficient of inbreeding of the Hereford bull, Beau Blanchard 362904, whose pedigree is given below:

- Beau Blanchard
  - Beau Mischief
    - Beau President
      - Beau Brummel
        - Don Carlos
        - Belle
      - Pretty L 25th
        - Lamplighter
        - Pretty L 16th
    - Mischievous
      - Lamplighter
        - Don Carlos
        - Lady Bird
      - Miss Charming 4th
        - Sylvester
        - Miss Charming
  - Blanche 23rd
    - Beau Brummel
      - Don Carlos
        - Anxiety 4th
        - Dowager 6th
      - Belle
        - North Pole
        - Beau Ideal 8th
    - Blanche 5th
      - Don Quixote
        - Anxiety 4th
        - Dowager 6th
      - Blanche 2nd
        - Don Juan
        - Blanche

253. Arrange the following individuals in the order of the prepotency which they will display (capital letters represent dominant factors):

Aa bb CC Dd EE Ff gg hh *aa Bb Cc dd EE ff Gg hh*
AA bb Cc DD ee FF GG Hh *AA Bb CC DD ee Ff GG HH*

REFERENCE ASSIGNMENTS

97. Compile a list of inherited traits in poultry, of which the method of inheritance has been established, stating the particular method of inheritance for each trait.

98. Compile a similar list for corn.

99. What were the probable wild ancestors of wheat; of corn; of peas; of cotton?

100. What were the probable wild ancestors of cattle; of the horse; of the dog; of swine; of poultry?

101. How does the milk production of superior pure-bred dairy cows compare with the average production of all cows at the present time?

102. Look up and describe a case, other than those mentioned in the text, of the mendelian inheritance of disease resistance in some animal or plant.

103. Give the pedigree of some variety of cultivated plants.

104. Give an example of an important strain of crop plants which was obtained by the isolation of a single pure line.

105. Give an account of the selection experiment of Castle and Phillips on hooded rats.

106. What is the effect of inbreeding on *Drosophila?*

107. State, in more detail than does the text, Jones's explanation of heterosis by means of linkage between dominant factors.

108. What physical traits are closely correlated with egg production in poultry which thus make it possible to pick out high-producing birds?

109. It is often held that the male in animals is more prepotent than the female. Criticize this belief and explain its origin.

110. Give an account of the life and work of Robert Bakewell.

CHAPTER XIII

INHERITANCE IN MAN

Perhaps the most striking fact which a survey of the laws of inheritance discloses is that *they apply with equal force to all sorts of living things*, and that laws established from a study of one organism have been found, with minor exceptions, to apply to all the rest. Most of the information has been obtained from species which may be grown experimentally in large numbers and in relatively small space, which breed rapidly, and which cost but little to maintain. The universality of the laws of inheritance, however, makes the geneticist confident that the principles established by a study of these animals and plants may be applied successfully to forms in which, because of various practical difficulties, there has been no extensive experimentation. Thus in the preceding chapter certain of the applications of the principles of genetics to the breeding of our races of cultivated plants and domestic animals were pointed out. In the present one the application will be carried still further, and the problems of inheritance will be considered as they are presented by the human race itself.

Man, exceptional in so many ways, is, nevertheless, essentially similar to those lower forms with which geneticists have been at work; and investigation has shown that many of his traits are subject to the same laws of inheritance. There is, therefore, justification in according special consideration to human heredity not because it is separate from the main body of genetic inquiry nor because it adds appreciably to a knowledge of general principles, but because of its bearing on all sorts of human problems and activities. Indeed, one of man's most immediate interests in genetics lies in the hope that it may assist in the interpretation and analysis of human traits and, more especially, that it may provide the basis for a sound and scientific program for racial betterment.

The problems of human inheritance must be studied by somewhat different methods from those employed with plants and animals. Direct experiments are obviously impossible, and

data must be accumulated by the less exact method of analyzing pedigrees and family histories. The traits studied in man, too, are somewhat novel, since those of most significance are not physical but *mental*, a type which cannot be readily investigated by experiments with the lower animals.

Investigations on Human Inheritance.—The study of human inheritance from the scientific point of view may be said to have begun in the last half of the nineteenth century with the work of Francis Galton, who was himself a member of a family which has produced a considerable number of distinguished men and women and which is often cited as a notable example of the inheritance of mental ability. Galton was born in 1822 and possessed versatile talents, acquiring in his earlier years a reputation as a mathematician, physician, meteorologist, psychologist, and explorer. He was attracted to the study of human inheritance through his observations on the repeated occurrence of high mental ability in certain families, and in 1869 published some of the results of these studies in a notable book, "Hereditary Genius." Scientific investigation of the inheritance of both mental and physical traits in man was greatly stimulated by this pioneer work, and it led directly to the establishment by Galton of the applied science of *eugenics*, through which he hoped that a knowledge of inheritance might be applied to the improvement of the racial qualities of man. The original impetus given by Galton to the study of human inheritance was greatly increased by the rediscovery of Mendel's laws in 1900, and under this new stimulation the knowledge of heredity in man has been much extended.

Human Traits.—In earlier chapters the inheritance of various human traits such as eye color, right- and left-handedness, stature, and color blindness, have been described as illustrative of some particular genetic principle. The chief problem at this point is to determine how far the general laws of inheritance which have been established for plants and animals apply to man; and, in particular, how those most important of all traits, the mental ones, are inherited.

To answer these questions a very considerable body of information is even now available, but much of it, unfortunately, is not as precise as it might be. In the absence of experimental data, such as is at hand for animals and plants, the geneticist must content himself with a study of crosses already made. Human families are also very small in comparison with the num-

bers produced by those lower species which have been chiefly investigated. On the other hand, the general interest in human traits is greater than in those of the lower organisms, and familiarity with them correspondingly more intimate. It is also possible to gather reasonably accurate information from a very large number of human pedigrees, and reliable records for some traits often go back for several generations. Some of the results which students of human inheritance have thus far obtained will be briefly reviewed here.

Racial Differences.—The most obvious of human differences, and ones very much in the foreground today, are those which distinguish the various races of man. The differences between Caucasian, Mongolian, Indian, and Negro, for example, are readily observable and it is evident that each race passes on its peculiarities from generation to generation by inheritance. Furthermore, in crosses between individuals of different races the offspring show resemblances to both parental types. In the offspring of negro-white crosses, for example, the influence of both parents is evident, and the various parental contributions tend to segregate among the individuals of later generations. Similarly, in the offspring of matings between Caucasian and Hebrew, Italian and Teuton, Polynesian and Caucasian, and many others, the influence of both ancestral types may be traced and often the specific peculiarities of each are seen to reappear later.

Indeed, these racial differences, although often complex in their expression and inheritance, are to some extent similar to those which exist between individuals. They differ from the simpler traits, which have become familiar, chiefly in the larger number of factor differences involved, for crosses between diverse races usually result in hybrid (F_1) types which are intermediate between the parents, and the later generations following race mixture are marked by great variability. Dominance is usually not noticeable, although some traits, such as the high nasal bridge which is characteristic of the Semitic nose, and the peculiar fold of the eyelid which is common in Mongoloid races, appear to rest on dominant factors. The inheritance of so-called "racial" traits is always difficult to trace exactly because they are seldom of the alternative type but usually differ in degree, and because by continued intercrossing following the movements of racial groups the present races of man have become very heterogeneous and variable.

Individual Differences.—The fact that racial differences are inherited is important, both theoretically and practically, but for the reasons given above, a study of them has added little to the knowledge of heredity. In order to gain more precise and definite information as to the genetic behavior of human traits, the inheritance of differences between *individuals* of the same racial stock must be studied as Mendel himself studied it, and the behavior of single, clearly recognizable characters from parent to offspring must be traced. In many cases, to be sure, these differences are also complex and difficult to analyze, but many of them are much simpler; and after pedigrees of individuals which differ in only a few traits have been studied, the methods of mendelian analysis can be applied, and human results can be brought in line with those which have been obtained from plants and the lower animals.

The Inheritance of Physical Traits.—Physical or bodily traits are far more favorable for study than mental ones, chiefly because of the greater ease with which they can be recognized and measured, and information about them is consequently more complete. Everyone has observed the similarity between members of the same family with regard to color of eyes and hair, height, weight, shape of features, and many other traits. Investigation has shown that in their hereditary behavior are represented most of the types of inheritance which have been discovered in plants and animals. Some typical examples will be briefly described.

Simple Traits.—Many character differences are very simple in their inheritance and are evidently due to a single pair of mendelian factors, one of which is dominant over the other. The best-known case of this sort is that of eye color. The iris of the eye displays a great variety of colors and patterns, but eyes may readily be divided into the browns, blacks, and other dark shades, in which the front of the iris is pigmented; and the blues, in which only the back is so. "Dark" eyes are dominant over blue ones, and the difference between them is probably due to a single factor. The inheritance of eye color is shown by the following typical pedigree chart[1] (Fig. 136).

A dominant character in such pedigrees may be recognized by the fact that it occurs in every generation and in at least

[1] The situation is apparently not always quite as simple as this, for there is evidence that factors influencing eye color may occasionally be sex-linked.

half (often more) of the individuals. A recessive character, on the other hand, usually appears in only a comparatively few individuals and often skips entire generations, cropping out here and there through the pedigree. It is evident that an individual showing a recessive character must be homozygous for it but that one showing a dominant trait may be (and in a mixed population more often is) heterozygous. A group of individuals displaying a given recessive trait is, therefore, pure genetically, as far as this trait is concerned, whereas among the members of a group showing a dominant character there may be many who are carrying a factor for its recessive allelomorph. In order for this recessive factor to express itself visibly, it must be brought in from both parents, and since this condition will

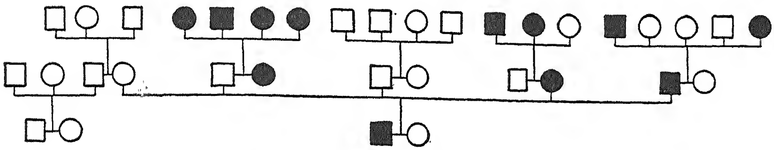


Fig. 136.—Pedigree showing the inheritance of eye color in man. Squares represent males and circles females. Individuals who are solid black have brown (dark) eyes; individuals merely outlined have blue eyes. This illustrates the method of inheritance of a typical dominant character and its recessive allelomorph.

be fulfilled rather infrequently, especially in populations where the trait is not common and where (as generally among human beings) close inbreeding is not practiced, it may actually appear but rarely.

Investigation has shown that there are many other physical traits which apparently are due to single mendelian factors and thus behave in their inheritance like eye color, although in many cases the interpretation of the facts may be made more difficult by the operation of modifying factors or other complications.

Various skeletal abnormalities, for example, are transmitted in this simple fashion. Among these is brachydactyly, a condition in which the hands and feet are short and stubby, and in which the arms and legs are also usually shorter than the normal. In the fingers and toes of brachydactylous individuals, the middle segment is extremely short and is fused with the terminal one so that the digits seem to have two joints instead of three. This condition has been studied in many different families and usually behaves as a simple mendelian dominant.

Another interesting abnormality affecting the digits is that of symphalangy or stiff joints, in which one of the joints is almost or quite immovable owing to a fusion between the bones. This also seems to be dominant in inheritance, and an instance of it remarkable for the length of time through which it has been traced is described by Gates from the work of Drinkwater as follows:

In the middle finger the joint between the middle and basal phalanges is only very slightly movable, the articular surfaces of the bones being enlarged, while in the ring and the little fingers there is no joint between the proximal and middle phalanges, these two being completely fused into one. All the fingers are movable at the distal joint, and both hands are alike. All the toes, except the hallux, are affected exactly like the ring and little fingers. This man's father and *his* mother are known to have had precisely the same abnormality. His father married twice, and one of the half-brothers shows it. The most interesting feature of this case is that A. T. is a direct descendant in the male line from John Talbot, the first Earl of Shrewsbury, who figures in Shakespeare's *Henry VI*, and was killed in battle near Bordeaux in 1453. Tradition has it that his thigh bone was broken while on horseback, and that when he fell from his horse he was killed by the blow of a battle-axe on the head. His body was buried in a tomb inside the church at Whitchurch, which was surmounted by a stone effigy. In 1874 the tomb was opened and repaired by one of his descendants. The skeleton was identified by the cleft skull and the fracture of the right thigh bone. The finger bones, when examined, showed the same ankylosis that exists in his modern descendants. On the stone effigy the fingers, which were somewhat damaged, also showed precisely the same thickening of the middle joint as described in his descendant. Clearly, then, this defect has been handed down for more than 500 years as a mendelian dominant, and the genealogy of the family shows that it must have been inherited through fourteen generations.

Zygodactyly, the fusion or "webbing" between adjacent fingers or toes; polydactyly, or the presence of extra fingers and toes; and "lobster claw," or "split" hands and feet, occur in various degrees, but like the other digital peculiarities mentioned, they are ordinarily dominant over the normal condition and seem to differ from it by a single mendelian factor.

Among other physical traits inherited in the same simple fashion is the white forelock or "blaze" in the hair, which occurs in a number of families and ordinarily behaves as a dominant. In one family the occurrence of this lock has been definitely

traced through six generations, and tradition carries it back to the son of Harry (Hotspur) Percy, one of the ancestors of the family.

Physiological Traits.—Aside from these structural characteristics, there is also evidence as to various functional ones. Among these is left-handedness. This character is usually recessive although there are some indications that dominance is occasionally reversed and that rarely the trait may be sex-linked. Hereditary deaf-mutism likewise seems to be recessive, two deaf-mutes when mated usually having deaf-mute offspring.

Diabetes insipidus, a kidney defect in which great quantities of urine are produced and excessive thirst results, is often inherited, in which case it is dominant to the normal condition. Bronchial asthma and "hay fever," on the other hand, when inherited ordinarily act as recessives.

Inheritance of Blood Groups.—Perhaps the most interesting of these physiological cases is the inheritance of the so-called blood groups. It has been found that the blood serum of certain persons will agglutinate or cause clumping of the blood corpuscles of certain other persons, and blood transfusions between such individuals may result in serious consequences. It has been possible to classify the many thousands of persons whose blood has been tested into four groups (I, II, III, and IV). Persons belonging to the same group do not agglutinate each other's blood; that is, serum from group I will not agglutinate corpuscles from group I, and so on. Blood from persons in group I will agglutinate the blood of persons in II, III, and IV, but is not agglutinated by their blood serum; group II blood agglutinates that from groups III and IV; group III blood agglutinates blood from II and IV, while group IV serum does not agglutinate the blood cells of any group. Considerable data on the inheritance of these properties of the blood show that individuals in group I are pure for two recessive mendelian factors (a and b) determining the *power to agglutinate* all other bloods; a confers the ability to agglutinate the corpuscle type represented by A; b likewise represents a specific agglutin for B corpuscles. Individuals in group IV contain at least one dose of each of the dominant allelomorphs (A and B) which make their corpuscles susceptible to agglutination by serum from the other three groups. Group II has A but not B, while group III has B but not A. The genotypes of the four groups are given in Table XX.

TABLE XX

Blood group	I	II	III	IV
Genotype...............	*aa bb*	*AA bb* *Aa bb*	*aa BB* *aa Bb*	*AA BB* *Aa BB* *AA Bb* *Aa Bb*

The inheritance of these two factors follows the simple scheme of independent mendelian assortment (Fig. 137) and the blood group of the offspring may, therefore, be predicted from a knowledge of the blood group of the parents.

Group IV × Group IV
Aa Bb *Aa Bb*

Sperm \ Eggs	*AB*	*aB*	*Ab*	*ab*
AB	*AB* *AB* Group IV	*aB* *AB* Group IV	*Ab* *AB* Group IV	*ab* *AB* Group IV
aB	*AB* *aB* Group IV	*aB* *aB* Group III	*Ab* *aB* Group IV	*ab* *aB* Group III
Ab	*AB* *Ab* Group IV	*aB* *Ab* Group IV	*Ab* *Ab* Group II	*ab* *Ab* Group II
ab	*AB* *ab* Group IV	*aB* *ab* Group III	*Ab* *ab* Group II	*ab* *ab* Group I

FIG. 137.—Showing the blood groups of the offspring expected from marriages between persons in blood group IV, each of which is heterozygous for both blood group factors *A* and *B*.

Many other traits seem to be due to a single mendelian factor, either dominant or recessive, but their expression is either so complicated by modifying factors, or the knowledge of them is so limited that they cannot be definitely placed in this group.

More Complex Traits.—Other traits are evidently transmitted in a more complex manner. In at least one group of related characters which includes albinism, the factors determining the

different grades of the trait probably form a system of multiple allelomorphs (page 165). Thus in the white races the degrees of pigmentation in hair and eyes with which the complexion of the skin is usually correlated may be arranged in a series of which the dark-haired, dark-eyed, swarthy types are at one extreme, and are connected with the opposite extreme of albinism through all intermediate degrees of brunette and blonde pigmentation. The darker grades appear to be dominant to the lighter, while all pigmented types are probably dominant to albinism.

No definite cases of linkage between factors have as yet been found in man, for there are twenty-four pairs of chromosomes, and the chances of the discovery of two factors in the same chromosome are, therefore, relatively slight. A number of traits have been found, however, which are sex-linked. In man, as in *Drosophila*, the female is homozygous for sex and possesses two sex or X chromosomes and the male only one, its mate being a Y (page 210).

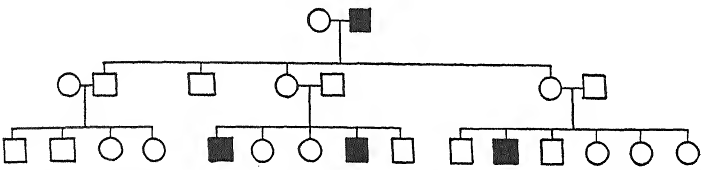


FIG. 138.—Pedigree showing the method of inheritance of color-blindness (black).

The most conspicuous of the sex-linked traits, which are probably traceable to factors located in the sex chromosome, is color-blindness, a characteristic inability to distinguish between certain colors, especially red and green. This defect is recessive to normal vision. Females may, therefore, be homozygous normal (X*C*) (X*C*); heterozygous normal or "carriers," (X*C*) (X*c*); or color-blind (X*c*) (X*c*). Males are either normal, (X*C*) Y, or color-blind, (X*c*)Y. A typical pedigree for color blindness is presented above (Fig. 138). It will be observed that the trait tends to appear only in certain of the males and is transmitted to them only through their mothers.

Hemophilia, or tendency to abnormal bleeding, is inherited exactly like color blindness, as apparently is Gower's disease, a form of muscular atrophy. Night-blindness is also sex-linked but may sometimes behave as a recessive and sometimes as a dominant with relation to normal vision. In a number of other

traits there is some evidence of the existence of sex-linkage, at least in certain families.

A number of characteristics have been shown to be due to two or more pairs of multiple factors and thus to show the "blending" type of inheritance so common in all quantitative traits. Most of the various size characters of the body probably show this form of inheritance. Davenport has analyzed the heredity of body height in man and finds that in general, shortness is dominant over tallness and that there may be two major factor-pairs which affect height. The same investigator has obtained evidence from crosses of negroes and whites that the skin color of the negro probably differs from that of the white man by the presence of several (possibly two) pairs of factors. Evidence on the inheritance of other quantitative bodily characters indicates that they are transmitted by a series of multiple factors and thus agree in their inheritance with similar traits in other organisms.

The Inheritance of Mental Traits.—More important than the physical characteristics of an individual, under the conditions of modern civilization, are his *mental* traits. If memory, tastes, and intellectual ability are all strongly inherited, then, indeed, heredity must play a decisive part in human affairs. Many will readily admit that bodily features are heritable, but look upon psychic traits as belonging to an entirely different category, quite beyond the control of genetic influences. Obviously, it is of great practical importance to determine whether or not this view is correct. A definite solution of the problems of mental inheritance is difficult, for a mental characteristic is a very hard thing to define and evaluate. Although psychology has made considerable progress in the development of methods for measuring all sorts of mental qualities and capacities, it is yet far from the point where a man's mind can be measured as accurately as his body. A still more serious difficulty which confronts the student of inheritance is that mental traits are subject to great modification by training and other environmental influences. The mind is plastic and educable to such a high degree as to lead to a conviction in the minds of many that differences in inborn genetic capacity are negligible in comparison with differences in kind and degree of education, so far as their effect on the ultimate mental attainments of an individual are concerned. Nevertheless, a very considerable body of evidence has been built up which

tends to show that, despite all this, inherited differences in mental qualities and capacities do, indeed, exist and are responsible for much of the evidedt variation in human mentality.

This evidence is derived from a number of different sources. Almost everyone can bring to mind from his personal acquaintance families in which high intellectual attainments, musical talent, business ability, mechanical genius, excellent memory or their opposites, or one of many other mental traits seem to "run in the family" and characterize some or all of its members generation after generation.

The Edwards Family.—Many families of this sort have been studied and their pedigrees carefully traced. Notable among them and often cited as an example of the importance of heredity in determining mental traits is the family of which Jonathan Edwards was a member. His grandmother, Elizabeth Tuttle, appears to have been a remarkable woman, both physically and mentally. She married Richard Edwards of Hartford, Connecticut, in 1667. From this union was born Timothy Edwards, a prominent Connecticut divine. His only son was Jonathan Edwards, a brilliant theologian, president of Princeton, and one of the foremost thinkers America has produced. The known descendants of this man numbered, in 1900, 1,394, including a vice president of the United States, three senators, several governors and members of Congress, thirteen college presidents, 60 college professors, besides principals of other educational institutions, 60 physicians, over 100 clergymen, missionaries, or theologians, 75 army and navy officers, 60 prominent writers, over 100 lawyers, and 30 judges. The four daughters of Elizabeth Tuttle and Richard Edwards also have among their descendants a long array of notable names.

Richard Edwards was divorced from his brilliant wife in 1691 and later married Mary Talcott, a woman who appears to have been of no more than ordinary ability. From this union came five sons and one daughter, and it is a noteworthy fact that none of their descendants seem ever to have risen above mediocrity. The difference between these two lines of descent, originating in two different women, seems to emphasize the importance of inheritance in mental traits.

Inheritance in Royalty.—Woods has made a careful study of European royal families, which present rather favorable material for this sort of investigation, since the mental and physical traits

of their members have been recorded much more fully than for ordinary men, and may be studied for many generations back. Woods found that the members of royalty who were outstanding because of their superior mentality do not appear scattered irregularly through the pedigrees but are for the most part found in a few groups of rather closely related individuals. One of these centers in Peter the Great of Russia, another in William the Silent of Holland, another in Isabella of Spain, and a fourth in Gustavus Adolphus of Sweden. There are groups, also, which show the occurrence of insanity, imbecility, and other more or less serious mental defects.

Hereditary Genius.—Francis Galton, in his "Hereditary Genius," studied the family histories of 977 eminent Englishmen and found that they were interrelated to a surprisingly high degree. An eminent man was far more likely to have eminent relatives than was an ordinary man, and superior ability seemed to be in great measure a family affair. Woods, in an analysis of 3,500 prominent Americans, found much the same situation, since one of this group was about one hundred times as likely to be related to a person of eminence as an ordinary individual chosen at random from the whole population. Men of genius, such as those who have been elected to the Hall of Fame, are even more closely interrelated.

Records of the scholastic attainments of fathers and sons, both in English and in American universities, point to the same conclusion. A superior father is more likely to have a superior son than is an average father, and certain families are characterized by high scholastic rank and some by low, generation after generation.

Families of Mental Defectives.—Much evidence of this sort has been accumulated showing not only the inheritance of high mental abilities but of mental deficiencies as well. Many human strains of apparently defective genetic constitution, mentally, have been traced through a considerable number of generations. Among these are the "Jukes," the "Kallikaks," the "Nams," the "Hickories," the "Ishmaelites," and others. Dugdale thus briefly describes the Jukes:

From one lazy vagabond nicknamed "Juke," born in 1720, whose two sons married five degenerate sisters, six generations numbering about 1,200 persons of every grade of idleness, viciousness, lewdness, pauperism, disease, idiocy, insanity, and criminality were traced. Of the total

seven generations, 300 died in infancy; 310 were professional paupers, kept in almshouses a total of 2,300 years; 440 were physically wrecked by their own "diseased wickedness;" more than half the women fell into prostitution; 130 were convicted criminals; 60 were thieves; 7 were murderers; only 20 learned a trade, 10 of these in state prison, and all at a state cost of over $1,250,000.

The Kallikaks are perhaps even more striking because of the difference in offspring of two women. Goddard describes this case as follows:

At the beginning of the Revolutionary War a young man, known in the history as Martin Kallikak, had a son by a nameless, feeble-minded girl, from whom there have descended in the direct line four hundred and eighty individuals. One hundred and forty-three of these are known to have been feeble-minded and only forty-six are known to have been normal. The rest are unknown or doubtful. Thirty-six have been illegitimate; thirty-three, sexually immoral, mostly prostitutes; twenty-four, alcoholic; three, epileptic; eighty-two died in infancy; three were criminal, and eight kept houses of ill-fame. After the war, Martin Kallikak married a woman of good stock. From this union have come in direct line four hundred and ninety-six, among whom only two were alcoholic, and one known to be sexually immoral. The legitimate children of Martin have been doctors, lawyers, judges, educators, traders, landlords, in short, respectable citizens, men and women prominent in every phase of social life. These two families have lived on the same soil, in the same atmosphere, and in short, under the same general environment; yet the bar sinister has marked every generation of one and has been unknown in the other.

All these facts are suggestive and certainly create a fair presumption that mental traits of all kinds are indeed inherited, but objection may be raised against all evidence of this sort that it tends to disregard the very powerful influence which environment and training may have in the development of mental qualities. Children born in the family of a Jonathan Edwards may from this very fact be expected to excel in mental accomplishment the chi dren of an uneducated laborer; and in the same way, illegitimate and outcast children will be far more likely to develop vicious traits than will those brought up in favorable environments. If the inheritance of mental traits is to be firmly established, lines of evidence of the sort thus far presented must be supplemented by others more precise and definite in character. Certain of these are at hand.

Psychic Inheritance in Animals.—First, there are a few cases in which the inheritance of psychic traits has been studied among animals. Many instincts, for example, seem clearly to be the result of inheritance rather than of training or imitation. There are innumerable instances among animals where an individual will carry out instinctive activities which it has never seen other animals perform and for which its only guide must be some inborn and inherited nervous mechanism. The nest-building of birds, the homing of pigeons, the tracking instinct of hunting animals, and many others are cases in point. Behavior of this sort may often be improved with training, but the basis of it seems clearly to be inherited.

More convincing are the results of crosses between animals which differ in some instinctive reaction. Castle has found that rats of races long bred in captivity are tame and easy to handle, whereas wild rats are not; and that if tame females are mated with wild males and the mothers isolated before the birth of the young, these young are almost as wild in temperament as wild rats, even though they have never been with wild ones. This seems clearly to be a case of the inheritance of a psychic trait.

Mendelian Inheritance of Psychic Traits in Man.—In man certain functional traits like left-handedness, Gower's disease, Huntington's chorea, or asthmatic tendencies, which must evidently have their basis in some nervous mechanism, are clearly inherited. Far more noteworthy from the present point of view,

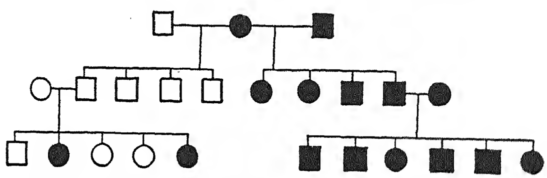


FIG. 139.—Pedigree showing the inheritance of feeble-mindedness (black). (*After Goddard.*)

however, is the behavior of congenital feeble-mindedness, a trait which is definitely a mental one and which acquires added importance from its social significance. Feeble-mindedness may, of course, be due to a variety of causes, among which are illness and accident, but a very large percentage of the cases are clearly traceable to heredity. In pedigrees involving such congenital feeble-mindedness, it ordinarily behaves like a typical mendelian recessive, appearing in about one-fourth of the off-

spring of two individuals known to be heterozygous for it, in about half those of a mating between a heterozygous individual and a feeble-minded one, and in all the offspring of two feeble-minded people. A typical pedigree involving congenital feeble-mindedness is presented above (Fig. 139). Feeble-mindedness occurs in varying degrees, and there are doubtless modifying factors affecting its character and intensity; but there seems to be one major mendelian factor which distinguishes it from normal mentality This is a rather definite case of a mental trait which in its inheritance is strictly comparable to many physical ones.

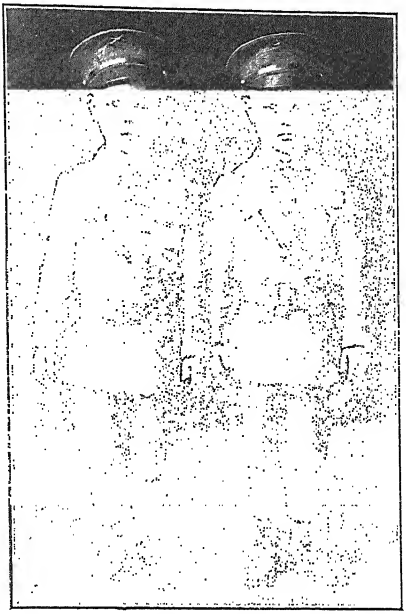


FIG. 140.—Identical twins. These two boys have exactly the same heredity since both developed from a single fertilized egg cell. (*From Journal of Heredity.*)

There are many other mental characteristics which display very evident segregation in a pedigree, cropping out here and there in certain individuals and being entirely absent in others. In most cases, however, the information at hand is too limited to determine the exact method in which the trait is transmitted.

Identical Twins.—These examples from animals and man are more convincing than those which were first cited, but they do not wholly meet the objection that the environment has a powerful, if not a preponderant, influence on most of our important mental traits. Interesting evidence on this point, however, is presented by a study of *identical* twins (Fig. 140). These are twins which have been formed by the division of the same fertilized egg, and they should thus possess precisely the same genetic constitution, in distinction from ordinary brothers and sisters or from non-identical twins, each of which has developed from a separate egg. Their genetic identity is evidenced by the fact that they are always of the same sex, and that in physical traits

they are so much alike that friends are sometimes unable to distinguish one of the members of a pair from the other. It is noteworthy that this resemblance extends also to general mental ability. Galton, who made a particular study of identical twins, found that even when the two members of a pair had been separated relatively early in life and brought up under different environmental conditions, certain similarities tended to persist with remarkable tenacity. Here dissimilarity of environment is apparently unable to change very materially the effect of similarity of inheritance.

Effect of Similarity of Environment.—Equally important, perhaps, is the inability of a similar environment to overcome genetic dissimilarities. It is a matter of everyday experience that the children of a family are usually very different from one another, not only in physical but in mental and temperamental characteristics. Even when the environment under which they are brought up is as similar as the same parents, the same home, the same school, and the same community can make them, these differences persist, and they seem to receive their only satisfactory explanation as due to inborn genetic differences, often complex in their inheritance, to be sure, but inherited in some way, nevertheless. This conclusion is emphasized still more when it is noted that identical twins are measurably more nearly alike than are ordinary brothers and sisters of the same family.

Correlation between Physical and Mental Traits.—The closeness of resemblance between individuals with regard to both physical and mental traits may be measured with a fair degree of accuracy by the method of correlation, and Thorndike and others have shown that the coefficient of correlation between children in the same family is about the same for mental as for physical traits. This fact is hard to explain if the environment is paramount in determining mental characteristics.

Experimental Evidence.—A final bit of evidence is important because it has been derived from attempts to solve this problem by direct experimental methods. If mental attainments are due primarily to the training which an individual has received, a group of individuals subjected to the same training ought to become more and more alike, mentally, the longer the training continues. Thorndike and others have shown, however, by careful measurements that for certain mental processes the

same degree of training not only does *not* tend to equalize individuals but actually makes them *more* diverse than they were before the training was given. A group of school children were measured as to their relative ability in adding a column of figures, and then were given an equal and considerable amount of practice in addition. After this they were tested again, and the bright ones and the dull ones were found to be relatively *further apart* than they were at the start. The genetically superior individuals were evidently *for that reason* able to profit more by practice than were the genetically inferior ones.

Therefore, the conclusion seems justified that to a very considerable degree mental traits, particularly those involving general ability and capacity, are affected by inherited factors. It must be remembered, however, that what is inherited is but a capacity or predisposition, and that precisely what will develop therefrom is due in great measure to environment and training. A person of moderate natural endowments who has developed them to the full extent of his capacity is often a more valuable member of society than one of higher gifts who, through indolence or lack of opportunity or training, has allowed them to lie fallow. No one doubts the efficacy of training in developing to full measure whatever particular mental potentiality an individual possesses, but it must be admitted that individuals seem to differ markedly in their potentialities. It is this fact that makes the science of human inheritance so important today.

Finally, the fact should again be emphasized that knowledge of the inheritance of human traits, both physical and mental, is still very elementary, and that it must be much amplified before it can be applied with confidence to the problem of improving the quality of the race. It is now possible, however, to see what such problems involve, and to make tentative suggestions for their solution, both of which subjects will be treated in the ensuing chapter.

QUESTIONS FOR THOUGHT AND DISCUSSION

180. In many families individuals eminent in one field (such as literature or statesmanship) will produce offspring who are also eminent but in a different field (such as science or the arts). In what sense may these superior attainments be said to be inherited and in what sense may they not be?

181. How would you distinguish by biometrical methods between a pure race and a mixed race, in man?

182. It has been found that for many traits the coefficient of correlation between husbands and wives is as great as that between brothers and sisters. To what fact do you think this is due?

183. What is the expected distribution of the two sexes in the case of non-identical twins in man?

184. What legal applications might be made of present knowledge of the inheritance of blood groups?

185. It has sometimes been maintained that the children born during the period of the parents' highest mental activity are superior to those born later or earlier. Criticize this belief.

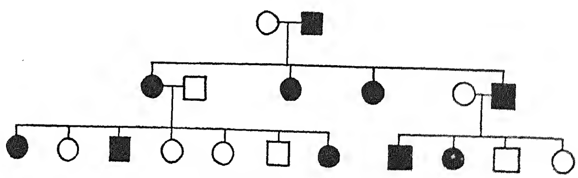
186. Do you think that there is any biological basis for the law of primogeniture? Explain.

187. It is estimated that the total *possible* number of *different* ancestors of each living person of English descent at the time of the Norman Conquest, is about 8,598,000,000. The total population of the British Isles was then only about 3,000,000, probably. What conclusion can you draw from these facts?

PROBLEMS

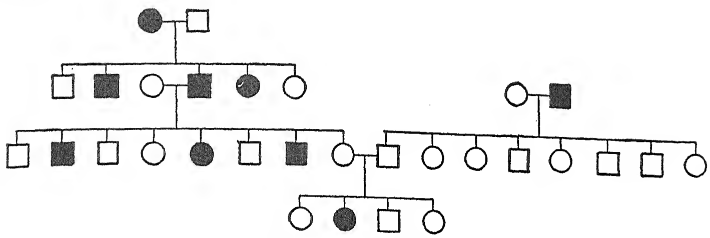
Note.—In the following twelve pedigrees the individuals which are solid black possess the trait mentioned. Squares represent males and circles females. Determine for each pedigree the *method of inheritance* of the trait in question (whether dominant, recessive, sex-linked recessive or other); and, so far as possible, determine for that trait the *genotype of each individual* in the pedigree.

254.



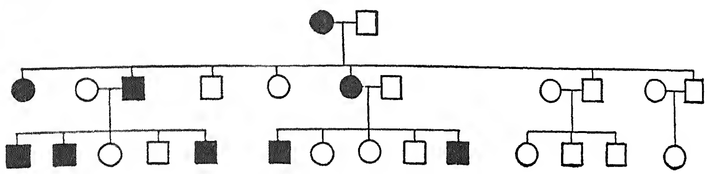
Right-handedness

255.



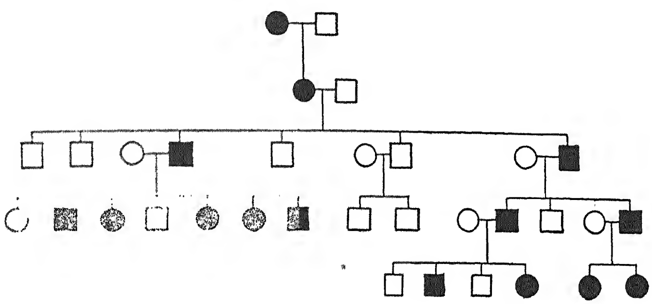
Left-handedness

256.



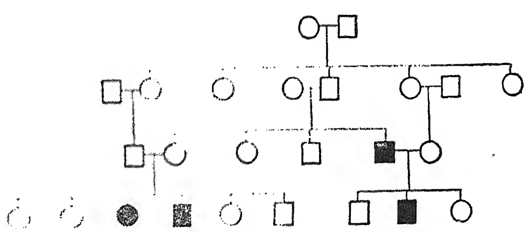
Polydactyly

257.



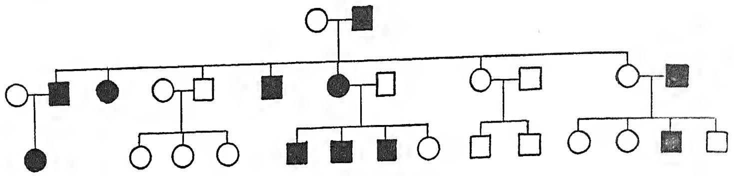
Monilothrix

258.



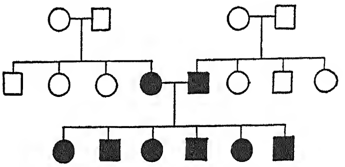
Muscle atrophy

259.



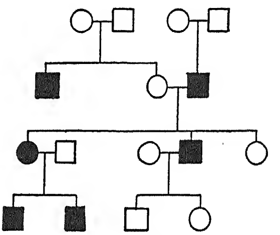
Short-sightedness

260.



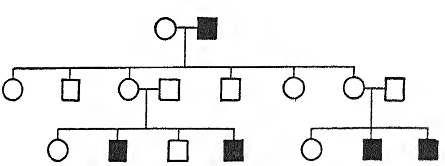
Feeble-mindedness

261.



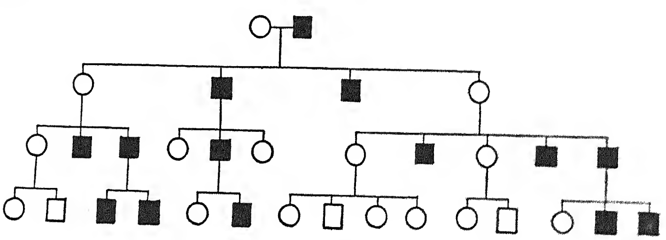
Color-blindness

262.



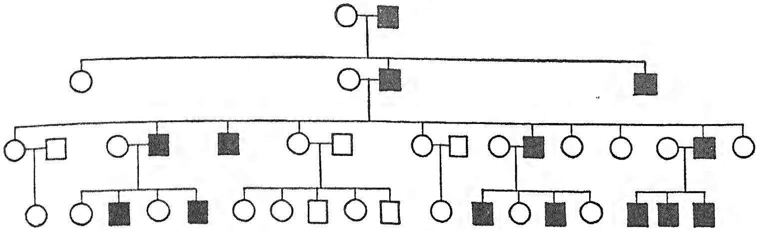
One form of ichthyosis

263.



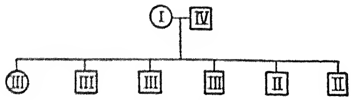
One form of white forelock

264.



Webbed toes

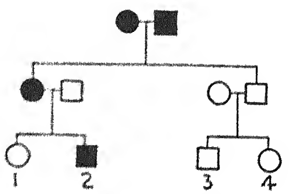
265.



Blood groups

Note.—In the following five pedigrees, calculate the probability that the trait in question will appear in the offspring of the various matings called for. Assume that these individuals have had no children and that the only indication as to their genotype is thus the occurrence of the trait in the pedigree. Assume further (unless there is evidence to the contrary) that individuals who have married into these families and who do not show the trait in question do not carry recessive factors for it.

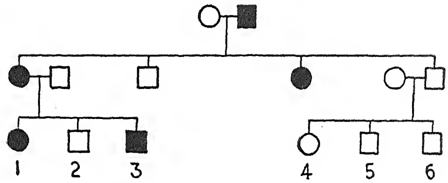
266.



Trait dominant

1 × 3
2 × 4

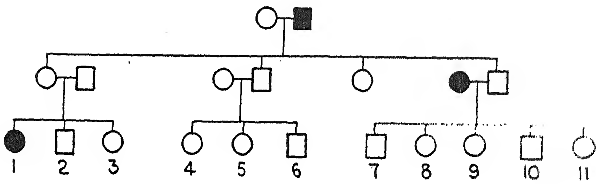
267.



Trait dominant

1 × 5
2 × 4

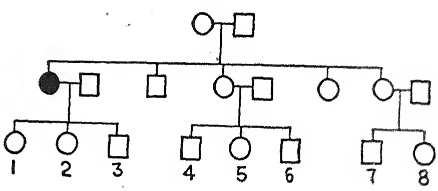
268.



Trait recessive

1 × 6
2 × 4
1 × 7
3 × 10
6 × 11

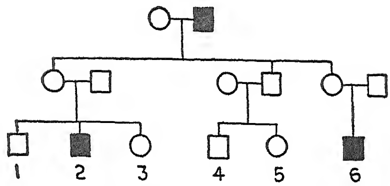
269.



Trait recessive

1 × 7
2 × 4
6 × 8

270.



Trait sex-linked and recessive

1 × 5
2 × 5
3 × 4
3 × 6
5 × 6

271. What are the chances that the first child from a marriage of two heterozygous brown-eyed parents will be blue-eyed? If the first child is brown-eyed, what are the chances that the second child will be blue-eyed?

272. Deaf-mutism may be due either to disease or to accident, or it may be inherited. Assuming that inherited deaf-mutism is recesssive, what offspring would you expect from the following marriages:

(1) Both partners with inherited deafness.

(2) One partner with inherited deafness, the other deaf through disease, but having no deaf relatives.

(3) Offspring from (1) married to a normal individual from normal stock.

(4) Offspring from (2) married to normal from normal stock; to deaf from deaf stock; to a person accidentally deaf.

273. A man's maternal grandmother had normal vision; his maternal grandfather was color-blind; his mother is color-blind; his father is of normal vision. What are the genotypes, as to vision, of the two parents and grandparents mentioned? What type of vision has this man himself? What type have his sisters? If he should marry a woman genotypically like one of his sisters, what type of vision would be expected in the offspring?

274. The mother of a right-handed, brown-eyed woman of normal vision is right-handed, blue-eyed, and of normal vision, and her father is left-handed, brown-eyed, and color-blind. This woman marries a man who is left-handed, brown-eyed, and of normal vision, whose father was blue-eyed. What chance will the sons of this couple have of resembling their father phenotypically?

275. To what blood groups will the offspring of the following crosses belong:

Group I × group II (homozygous).
Group I × group II (heterozygous).
Group I × group III (homozygous).
Group I × group III (heterozygous).
Group I × group IV (homozygous).
Group I × group IV (heterozygous) for both factors.
Group II (heterozygous) × group III (heterozygous).

276. What are the genotypes of the parents, as to blood groups, in the following matings?

Mating No.	Parents	Offspring
1	I and II	One-half I, one-half II
2	II and III	All IV
3	II and III	One-half II, one-half IV
4	II and IV	Three-fourths IV, one-fourth III
5	II and IV	Three-eighths IV, three-eighths II, one-eighth III, one-eighth I
6	I and IV	One-fourth I, one-fourth II, one-fourth III, one-fourth IV
7	IV and IV	Nine-sixteenths IV, three-sixteenths III, three-sixteenths II, one-sixteenth I

277. If the blood groups of one parent and of the children are known, it is sometimes possible to determine to what group or groups the other parent must have belonged. Determine, so far as possible, the blood group to which the unknown parent must have belonged, in the following families:

Family No.	Blood group of known parent	Blood group of children
1	III	II
2	I	IV
3	II	II and III
4	III	III and IV

REFERENCE ASSIGNMENTS

111. What were the probable physical characteristics of the primitive human stock from which the races of today have descended?

112. Compile a list of inherited mental traits in man; of inherited physical traits.

113. Compile a list of the known sex-linked traits in man.

114. Describe the "Hapsburg lip" and trace its occurrence in European royalty.

115. What is the present status of knowledge with reference to the inheritance of stature in man?

116. Two kinds of dwarfs are recognized, achondroplasic and ateliotic. How do these differ?

117. Give an account of the history of the mutineers of the "Bounty."

CHAPTER XIV

THE PROBLEMS OF EUGENICS

Heredity has long been acknowledged as one of the important forces at work in causing the evident differences among men in mental and physical traits. The respect accorded by all peoples to considerations of birth, family, rank, and race provide ample evidence of this fact. The relation of heredity to the problems which have arisen in modern societies, however, has only recently been appreciated. There are perhaps two chief reasons for this tardy realization. The first is that, in spite of the recognition of the importance of heredity, there has always been a general feeling that environment is more important in determining not only the destinies of the individual, but of races and societies as well. The second reason is that until comparatively recent times there has been no exact knowledge of how heredity works, and its significance could not be correctly gauged.

It has become more and more apparent, however, that the environment is not of exclusive or paramount importance in determining the characters of individuals, or of races or societies. It is but one agent in the interaction which produces the characters in question; the other and fully as important one is the inborn nature of the organism, as determined by its inherited constitution. This conclusion has become evident not only from the results of experimentation with the lower animals and plants, but it has been reached by students of man himself. Such evidence as was presented in the last chapter leaves no doubt that many human traits, both physical and mental, are inherited in accordance with the same laws which govern the transmission of characters in animals and plants. A realization of these facts led in the latter half of the nineteenth century to an insistence on the part of a small group of thinkers, of which Francis Galton was the chief, that all efforts to deal with the problems of modern society and especially all proposals for the improvement of the race itself must concern themselves not only with improvements in education, economic conditions, and other

commonly recognized environmental factors, but must include as a basic part of their program the improvement of the genetic constitution of the individual. Such considerations have led to the modern *eugenics* movement which has as its object the improvement of the inborn qualities of man.

Eugenics.—The term *eugenics* was proposed in 1883 by Francis Galton, who may be said to have founded the movement as it is known today. He had been led to a realization of the rôle of heredity in determining mental traits through his studies on hereditary genius, of which a brief description has been given in the preceding chapter. On the basis of his knowledge of human inheritance, Galton made definite proposals for increasing the proportion of physically and mentally able individuals in the population, and for decreasing the numbers of unfit and defective. Realizing that actual facts about human inheritance were the first requirements for a sound program, he founded a laboratory for the collection and analysis of such data. After his death in 1911 this became the Galton Eugenics Laboratory of the University of London under the direction of Professor Karl Pearson. The movement has now spread to all parts of the world, and has attracted considerable popular interest and support. In the United States the chief agency for the accumulation and study of data on human inheritance and eugenics is the Eugenics Record Office which for fifteen years has been under the direction of Dr. C. B. Davenport. Eugenics has now become firmly established as an applied science utilizing the results from general genetics and especially from human inheritance and sociology.

The Problems of Eugenics.—An unprecedented increase in the population of all civilized countries has taken place within the last century. The chief problem with which eugenics is concerned is presented by the fact that this increase has been *differential;* the rate being *lowest* among that portion of the population which is mentally most highly endowed, and *highest* among the defective and less well-endowed classes. Each of these classes constitutes a relatively small fraction of the population, but from the one are recruited many of the leaders in those pursuits which are regarded as of greatest social value, such as the arts, the professions, and government; while from the other has come a large proportion of the inmates of asylums, prisons, almshouses, and institutions for the feeble-minded.

The chief reason for this differential increase in numbers is that the *birth rates of these two classes have become markedly different*, those individuals of the lowest social value having consistently the highest birth rate. The causes of this differential birth rate are probably economic rather than biological. One of the chief reasons for the decreasing birth rate of the highly endowed fraction of the population has probably been the great increase in actual wealth which has marked the period since the introduction of the present industrial system and which has conferred on a small portion of the population the leisure and the desire for higher education, and the consequent postponement of marriage. The ambitious and well-endowed have often been encouraged, by economic conditions, to seek a higher and even a luxurious standard of living, and as a means to this end to avoid the inconvenience and expense of rearing children. Their birth rate has fallen because they marry late and because they voluntarily limit the size of their families.

These restrictive factors have not operated to restrict the birth rate of the defective elements of the population. Social advances have been at once responsible for an improvement in the condition of such unfortunate persons and for the increase in their numbers, for through the increasing care exercised by society for the benefit of the weak and subnormal, it has become possible for many of these to survive and multiply, who under less civilized conditions would be eliminated by natural selection. Ambition and foresight are weak among these groups, the birth rate is unrestricted, and they tend to increase at a high natural rate.

The Increase of the Defective.—At the bottom of the human scale stands a group of individuals who are so poorly endowed that almost everyone would agree that the elimination of their stock from society would be desirable. These are the congenitally defective, who are either unable to care for themselves and must, therefore, be a burden to more fortunate individuals, or who are so antisocial in their instincts that they prey on society as a whole.

Notable among this group are the feeble-minded. The Jukes and the Kallikaks have already been briefly mentioned, but there are many other families in which weak mentality is common and in which it is evidently passed on by inheritance from generation to generation. Aside from such whole pedi-

grees which are notoriously defective in this regard, there are thousands of cases of congenital feeble-mindedness which persistently crop out in families where the great majority of the members are apparently normal. There are probably over 300,000 feeble-minded in the United States today, the great majority of whom owe this defect to inheritance, although many have acquired it through accident or disease. There is good evidence, as has been pointed out, that congenital feeble-mindedness is recessive to normal mentality (or at least that there is one main factor difference between the two), so that there must necessarily be very many more individuals who are normal but carry recessive factors for this defect than there are who actually show it. It is impossible to compute accurately the number of such "carriers" but they have been roughly estimated at several million. So long as such individuals marry into stock which is free from this defect, it will not appear in their offspring, but it will do so if they intermarry or mate with persons like themselves.

Frequently associated with feeble-mindedness in inheritance seem to be other defects, such as epilepsy, chronic alcoholism, extreme sex offense, and similar congenital defects which are present in many thousands of individuals, and which often seem merely to be different expressions of the same underlying genetic defect. Of epileptics alone there are between 100,000 and 200,000 in the United States today.

Probably the most conspicuous and familiar mental defect is insanity. This may be induced by environmental causes, but in a great many cases it seems to be the result of inheritance. Because of the fear which the insane commonly inspire and the great inconvenience of caring for them in private homes, they have been much more fully segregated in institutions than have the feeble-minded. Over 200,000 insane are now receiving such care in the United States. There must also be a very large body of individuals who, although normal themselves, carry factors for this weakness.

The large population of jails and other penal and reformatory institutions may not belong to a "criminal class," as has been maintained by some criminologists, but psychiatric examination of the inmates of these institutions has shown in many cases a very considerable proportion of feeble-minded individuals; and although many criminals are doubtless the victims of a poor environment and unfortunate circumstances and are not inferior

biologically to the normal population, there is reason to believe that the weak inhibitions and antisocial dispositions which have resulted in their detention are closely related to the genetic defects in mentality which lead to congenital feeble-mindedness and insanity. Certainly that portion of our population which consists of repeated offenders and habitual criminals would be admitted by almost everyone to be a group with which society could well dispense.

Finally, the paupers, ne'er-do-wells, tramps, beggars, and others who are unable or unwilling to support themselves and must depend, for a part of the time at least, on institutional aid, are more numerous than is often thought and undoubtedly owe their low estate in many cases to defective inheritance. Improved economic and social conditions would doubtless reduce the numbers of this group by removing from it those who are victims of circumstance or lack of opportunity, but it is to be feared that even under the most favorable surroundings there would still be a great many individuals who are always on the border line of self-supporting existence and whose contribution to society is so small that the elimination of their stock would be beneficial.

These various classes differ a good deal among themselves, but they are all preponderantly defective or *dysgenic* to such a degree that if any element were to be eliminated from the country's racial stock, this group would certainly be included. Just how numerous these congenitally defective individuals are, it is difficult to say, but a conservative estimate for the United States places them at between 1,000,000 and 2,000,000, with the probability that there are 10,000,000 individuals who in their genetic constitution are carrying factors for some mental deficiency.

From the purely economic viewpoint, the burden which this large group of defectives entails is considerable. Most of the already great expense of maintaining institutions for the feeble-minded, the insane, and other defectives, together with a large portion of the cost of prisons and other penal institutions, as well as almshouses and similar sources of charitable relief, is expended in the care of this dysgenic element of the population. The total amount of this bill is enormous.

It may be argued, however, that society has always had defective and inferior elements within itself, but has, nevertheless, managed to survive and even to progress, and that the existence

of such individuals is unfortunate but does not present a problem serious enough to call for any very drastic remedy. The situation is not a constant and static one, however, which has long existed in its present state, but is apparently becoming steadily more acute. This is again indicated most forcefully by its economic aspect, for investigation shows that the care of these defective elements in our population is requiring a sum which is steadily increasing, not only actually but relatively. Part of this increase doubtless results from the better care given these unfortunates now than ever before, but much of it seems to be due to the fact that year by year the members of these dysgenic classes are coming to constitute a larger and larger element of the population. A part of this gain, in turn, notably the increase in insanity, is traceable to the more strenuous and complex life which we are leading and to other environmental causes, but most of it results from the fact that defectives are multiplying faster than normal persons. Definite figures on this point are hard to get, but it is safe to say that the birth rate among the feeble-minded is twice that of the professional classes.

Suggested Methods for the Elimination of the Defective.— Granting that society can decide just which individuals it wishes to eliminate as genetically inferior—a task which will prove to be a very difficult one—how shall it proceed to eliminate them?

For the efficient performance of this task a sound and well-informed public opinion in the matter is the first and most essential requirement. The knowledge of human inheritance is not yet great enough to warrant a vigorous propaganda for specific remedies, but students of genetics can at least endeavor to assist in stimulating a thoughtful interest in the problem in order that its solution may be approached in a sane, unprejudiced, and intelligent fashion. Meanwhile, there are several definite proposals with the essential points of which everyone should be familiar.

It is obvious that the great bulk of the defective population cannot be eliminated by the drastic methods which obtain in animal and savage societies. Death will ultimately remove the defective individuals themselves, and society must confine its eugenic efforts to preventing them from leaving offspring to perpetuate their undesirable traits. If this can be successfully accomplished, the defective strains will eventually die out, and the problem will be solved with the least possible hardship.

An obvious method of achieving this end is to prohibit by law the marriage of certain classes of individuals. Precedents for such prohibition have long been established for closely related individuals, although it is doubtful if public opinion would support any drastic restrictions on choice of mates. As to whether legal prohibition would actually accomplish the desired end, however, is a matter of considerable question, for the class of individuals at whom it would be directed are less amenable to law than are normal members of the population, and laws of this sort would be difficult to enforce. Even if they were complied with, they would by no means solve the problem, for the proportion of illegitimate births among defectives is high, and even if marriage was forbidden them, they would doubtless still leave behind a very considerable number of offspring.

The most direct method which has been proposed is to render these defective individuals incapable of reproduction. An operative technique has been developed which is applicable to both sexes and which does not interfere with anything in the normal life of the individual except his procreative ability. This method, however, requires the enactment of laws which, since they may be construed as limitations of personal liberty, have reached the statute books in few cases. Where such laws are in force, a small number of operations have been performed on criminals and insane persons, but the laws in some instances have become dead letters. There has also been found a good deal of disinclination on the part of medical officers and others in authority to designate individuals for sterilization, and it is questionable whether public opinion at present would tolerate any very extensive use of this method of preventing the reproduction of defective types.

A method which combines elimination of defective stock with care of the living defectives is the segregation of these individuals in institutions, colonies, or other groups, the sexes being kept entirely separate from one another. By this means the mating of the defectives among themselves or with normal members of society is prevented, and they themselves receive good care and are given an opportunity for such development as their limited powers allow. Under the "colony plan" which is being tried in New Jersey, imbeciles, morons, and idiots are grouped in colony units which are in part self-supporting through the practice of agriculture in the summer and of simple trades in the

winter; and these colonies may be moved about from place to place, the men clearing and draining land and performing other services for which unskilled labor is sufficient, thus using "waste humanity to reclaim waste land." The women can also carry on many useful occupations. These defectives are thus enabled to make some contributions to society, but they are successfully prevented from leaving offspring behind them.

The problem of segregation, however, is a difficult one. Our insane asylums and penal institutions of various sorts segregate many individuals, but this is often for a comparatively short period and thus restricts but little the opportunity for reproduction. Systematic segregation of mental defectives throughout the reproductive period is now applied to only about 10 per cent of this class in the United States. To extend this care to all of them would involve great expense and frequent legal difficulties, but the gain would perhaps in time warrant the economic outlay. It would by no means solve the problem to segregate all the living defectives, for, as has been pointed out, a very considerable proportion of the population, perhaps as high as 10 per cent, are carrying recessive factors for various defects; and among their offspring, for generations to come, defective individuals will continue to crop out. It would take a very long time for even the most careful and thorough segregation to eliminate this defective inheritance, but much of it could be weeded out in a few generations, and the present increase could certainly be checked. Segregation on the whole seems to be the most humane and effective method of restricting the multiplication of the dysgenic classes, and if society is willing to bear the expense involved, it will probably be adopted more and more widely.

An enlightened public conscience will be of the greatest service in this regard and is already making itself felt. Individuals who know that they carry factors for mental and physical defects are beginning to realize that their right to produce offspring is qualified by society's right to maintain the soundness of its stock, and much undesirable human material will in time thus disappear. This in general would mean the application to other groups of the voluntary limitation of births which is chiefly responsible for the low birth rate among the upper classes.

The control of the defective element in our populations thus offers many difficulties. These defectives are still in a small

minority, however, and when the increasing economic burden which they entail becomes sufficiently great, this very pressure will force the attention of society upon the problem, and it will be more thoroughly studied. The discovery and dissemination of the facts of inheritance, the increase in accuracy and facility of methods for distinguishing hereditary from purely environmental traits in man, and the intelligent appreciation of the problems involved may be considered as the most effective contribution which genetics can make to this problem of eugenics.

The Decrease of the Highly Endowed.—Much more difficult is the problem presented by the relative decrease in numbers of that portion of the population which seems genetically to be the most highly endowed. Attainment of a position in this class may frequently be the result of accident or of an unusually favorable environment or training, but in many cases it seems to be due to inborn capacity which is transmissible to offspring. It should be remembered, however, that, even if it is present, such a genetic constitution is unable to express itself in superior attainments unless the environment is favorable; and there is every reason to believe that very many individuals exist who are not notable by their own performance but, nevertheless, possess an inheritance of which they have never been able to take advantage. In any case, attainment rarely equals possibility, for there are few who ever develop to the full limit of their capacity.

The relative decrease among the intellectual classes is well illustrated by studies which have been made of the families of American college graduates. It would be untrue to claim that all members of this class are superior in native gifts to the noncollegiate population; but it is, nevertheless, a distinctly selected class by virtue of the fact that its members have had to undergo, in the process of their long educational career, a rather rigid testing which has eliminated from among them all who are not reasonably well-endowed mentally. It also contains many men and women of great brilliance. For these reasons, therefore, its average may safely be regarded as distinctly above the average of the population as a whole in native mental endowments.

A study of the families of graduates of men's colleges, women's colleges, and co-educational institutions shows that in all of them the birth rate is less than in the population as a whole, and that in many cases it is not high enough even to maintain existing

numbers. In the case of Harvard and Yale, where class records are available for many years, the birth rate has been found to be steadily falling in recent years until at present the average number of surviving children per graduate (in families which are completed) is estimated at about 1.9. In other words, these college graduates are not only failing to multiply as fast as the rest of the population, but are not even holding their own numerically, and at the present rate of reproduction their stock will actually have died out in a few hundred years. Such figures as are available show that the graduates of most women's colleges have a birth rate much below that of non-college women, and their stock is even further from maintaining itself than is that of the graduates of men's colleges.

The same thing is apparently true of educated people in general. Cattell's analysis of 1,000 American men of science, for example, shows that the average number of children in their families is somewhat less than two.

Whole racial groups may show a similar drop in birth rate and are thus apparently doomed to extinction. The old "American" stock in New England is the most commonly cited example of this. The day of large families, so universal among the ancestors of this portion of the population, has gone by, and this stock is today failing to maintain its relative position as compared with the other elements of the New England population (chiefly foreign-born), and in many cases is actually dying out. Crum's genealogical studies among old New England families bring out this point clearly. Table XXI from his data shows the average number of children per family from 1750 to 1879 among over 12,000 families which he examined.

Table XXI

1750–1799	6.43
1800–1849	4.94
1850–1869	3.47
1870–1879	2.77

Why is it that those individuals who are apparently more highly endowed than the average and are thus the most valuable human stock are failing to perpetuate themselves? The reasons are apparently not physiological—for there is no evidence that potential biological fertility is related to mental endowment—but are mainly economic in character. Educated people, in

general, have a keen desire for a higher and higher standard of living; and this desire has been partly fulfilled and still further stimulated by the increased financial success which superior ability usually commands. The rearing of a family interferes very seriously with the pursuit of such an attractive mode of life. Not only is the bearing of children a physical hardship, but the care and energy which must be devoted to their upbringing often prohibits the realization of many things which are highly desirable in themselves.

The expense involved in bringing up children in conformity with intelligent modern standards of health and education is also so great that very many people cannot afford to rear more than two. The costs of food, of clothing, of medical attention, of domestic care, and especially of education have not only increased, but are by far the greatest among the higher levels of society, where children are no longer an economic asset but a serious economic liability.

For these reasons a large number of children is not desired by most people among whom the standard of living is high, and these people have, therefore, voluntarily limited the size of their families to the number of children which they feel able to rear without giving up their present standard of living. A similar economic pressure is also making itself felt in all levels of the population, though by no means as strongly in the lower ones, for here the necessary living standards are lower and less vigorously maintained, and the incentive to reduce family size is, therefore, not as great. This circumstance, together with the fact that voluntary limitation of births is as yet but little understood and practiced among them, and that there is often a distinct prejudice against its use, results in the maintenance of a birth rate which, although it has fallen somewhat, is now very markedly higher than that which prevails in the professional classes.

Aside from this differential birth rate, the age at which marriage and reproduction take place plays an important though less obvious part in determining the relative rate at which these various classes are multiplying. The long and expensive education which many individuals of the highly endowed group must undergo necessarily delays the time at which they can marry and begin to raise a family. Even if the birth rate in both groups is equal, and if it is high enough to produce an actual increase,

the one which marries early and has four generations per century will obviously gain markedly in numbers over one which marries late and can have only three. It has been estimated that every couple capable of reproduction should produce on the average 3.7 children, if their stock is to be maintained at its present number. Many elements of the population are certainly not reproducing themselves at this rate, and will in time disappear.

A solution of this problem is much more difficult to arrive at than is that of the increase of the defective. It is far easier to prevent the reproduction of a given class than it is to induce a group of individuals to reproduce itself more rapidly. The eugenic program is much less precise in this, its positive or constructive aspect, than in its negative or restrictive one. It should again be emphasized that it is just as difficult to recognize the genetically superior human stock as it is the genetically inferior, and that until knowledge, both of the relative rôles of heredity and environment in the development of human traits and of the manner in which these traits are inherited, is more exact, it will not be possible to deal very intelligently with the problem.

Proposals for Increasing the Highly Endowed.—Various proposals have from time to time been made, however, which admittedly aim at accelerating the reproduction of the highly endowed or which might tend to have that effect. The partial exemption from taxation of a man with a family as compared with an unmarried man (as in the administration of our Federal income tax) is a case in point. More rarely an actual bonus is paid for every child above a certain number, as is done in France today. Taxes on bachelors have been proposed (to induce them to marry, perhaps), as have state pensions for young people who are still receiving their education and are as yet financially unable to support a family, but whose marriage and early parenthood would be advantageous to society. All these proposals are more or less unsatisfactory because no very definite methods have been found for applying them to individuals who are clearly superior genetically. Some couples, for example, should not be encouraged to rear large families, and some bachelors had best remain so, but clear-cut distinctions between these and individuals or matings of greater social value are very difficult to make. As knowledge increases, however, it may become possible to make an intelligent use of economic measures of this sort which may have positive eugenic value.

The ultimate solution of the problem, however, cannot be attained by legislation, but must work itself out through the cultivation of an enlightened and conscientious public opinion, which will encourage individuals of good natural endowments to raise families large enough so that their valuable heritage may be transmitted undiminished to later generations. This in time will stimulate an individual to feel his responsibility to his family, not only in maintaining its numbers but also in marrying into another stock of equal or superior endowments. Anything which will tend to make marriage a more serious affair and one not to be entered into lightly will be of value in rendering the choice of a mate somewhat more deliberate and thoughtful, and thus in making it more likely that superior stocks will be united rather than dissipate themselves in matings with inferior ones. Evidence is not lacking that public opinion and private conscience are awaking to the problem and that the intelligence and moral sense of the human race will succeed in solving it.

Eugenics is concerned so intimately with many of the major problems of today that these cannot be studied without an understanding of human heredity and the part it plays in society. The success or failure of democracy, the menace of war, immigration policies, and the relations between the races, all have important eugenic implications. In considering the bearing of human inheritance on all these questions, however, it should always be remembered that man is enormously educable; that even a relatively poor genetic constitution may respond to the proper type of environment and training; and that individuals, as well as races, differ markedly in their native endowments, almost all of them having some contributions of value for humanity as a whole. For this reason all attempts to develop a standardized "superman" by an application of the methods of animal breeding, a proposal which has brought the term "eugenics" into disrepute with many, is bound to fail. For a long time the only accomplishment to be expected will be the elimination of the obviously defective and the encouragement of the undoubtedly well-endowed, letting an intelligent eugenic conscience take care of the rest. Eugenics, after all, is but one program for human betterment, and in the zeal for an application of the principles of genetics to human affairs the reformer must not lose sight, as some enthusiasts have done, of the importance and the value of other methods which lead to the same goal.

QUESTIONS FOR THOUGHT AND DISCUSSION

188. In what important respect is the goal of a breeder of a given race of livestock different from the eugenic goal of the human race?

189. What is the eugenic importance of an increased interest in genealogy?

190. Measles and chicken pox killed thousands of natives of the South Sea Islands at the first coming of the white men, but these diseases are rarely fatal to Europeans. Explain these facts.

191. Dean Inge estimates that between 1800 and 1900 the population of England increased 300 per cent, but only 30 per cent between 1700 and 1800. This statement is probably true for most European countries. Why was this so?

192. Why is marriage among the wage-earning classes usually earlier than among the professional classes?

193. What is the probable eugenic effect of old-age pensions?

194. What is the probable eugenic effect of "motherhood" pensions?

195. What is the probable eugenic effect of immigration in the United States, and of the present system of restricting immigration?

196. Do you think that a legal prohibition of marriages between cousins is eugenically sound? Explain.

197. What is the probable eugenic effect of pedagogical and ecclesiastical celibacy?

198. What do you think has been the usual eugenic effect of capital punishment for political crimes and for heresy?

199. The Napoleonic wars are said to have reduced somewhat the average stature of the French people. To what might such a result be due?

200. What do you think is the eugenic effect of modern warfare? Does this differ from the eugenic effect of warfare in the days of small professional armies? Explain.

201. In the case of several women's colleges the graduates who were of superior scholarship while in college have a markedly lower birth rate than other graduates. What explanation can you suggest for this fact?

202. The quality of the old "American" stock in the rural districts of New England is said to have deteriorated during the past century. What factors might account for such deterioration?

203. A relation is sometimes traced between the Inquisition, which was particularly active in Spain, and the decline of Spain as a great

power which took place not long afterward. What basis do you think there may be for this?

204. What is the probable eugenic effect of greatly increased facilities for transportation?

205. What is the probable eugenic effect of interracial matings?

206. What was the probable eugenic aspect of the selective draft as conducted in the United States during the last war?

207. What is the probable eugenic effect of compulsory education?

208. What will probably be the eugenic effect of equalizing opportunity and education for women and men?

209. What is the probable eugenic effect of prohibition?

210. Which do you think are eugenically superior, separate colleges for men and for women, or co-educational institutions? Explain.

211. Which do you think is eugenically superior, a city environment or a country one? Explain.

212. What is the eugenic aspect of the contest between aristocratic and democratic systems of government? Which do you think is eugenically superior? Explain.

213. Which do you think is likely to be more successful, a civilization where various racial types live side by side but maintain their racial purity by breeding only among themselves, or one where these racial types interbreed freely? Explain.

214. What advantages and what disadvantages will a genetically mixed (highly heterozygous) population be likely to have as compared with one that is relatively pure genetically?

215. What relation is there likely to be between the relative birth rates of nations and wars arising between these nations?

REFERENCE ASSIGNMENTS

118. Give an account of the origin of the eugenics movement.

119. What was the theory of Malthus with regard to population?

120. Is modern man physically superior or inferior to the men of the middle ages?

121. Cite a family history in which there is frequent occurrence of exceptional ability and name at least six notable members of it.

122. Give an account of some family in which the frequent occurrence of eugenical defects has been reported (the "Nams," "Hickories," "Ishmaelites," or a similar family).

123. Distinguish between biological and social inheritance.

124. Criticize the theory of Lombroso as to the existence of a "criminal type."

125. Describe the New Jersey "colony system" for the segregation and care of feeble-minded.

126. What eugenic laws has your state on its statute books?

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